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# A tragedy of the common

Wild bird and insect decline in the current era

Caspar A. Hallmann

Caspar, A. Hallmann. 2019. The tragedy of the common: Wild bird and insect decline in the current era. PhD Thesis, Radboud University, Nijmegen, The Netherlands.

ISBN 978-94-028-1774-4

PRINTED BY IPSKAMP PRINTING <https://www.ipskampprinting.nl/>

Cover image of foraging Common staling (*Sturnus vulgaris*) by Jouke Altenburg.

Images throughout the dissertation by Jouke Altenburg and Martin Sorg

The research encompassed in this thesis was conducted at the Institute for Water and Wetland Research (IWWR), Departments of Experimental Plant Ecology, and Animal Ecology and Physiology, Radboud University, with the support of NWO grant 840.11.007.

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# A tragedy of the common

Wild bird and insect decline in the current era

Proefschrift

ter verkrijging van de graad van doctor

aan de Radboud Universiteit Nijmegen

op gezag van de rector magnificus prof. dr. J.H.J.M van Krieken,

volgens besluit van het college van decanen

in het openbaar te verdedigen op dinsdag 12 november 2019

om 16:30 uur precies

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Doctoral Thesis  
to obtain the degree of doctor  
at Radboud University Nijmegen  
at the authority of the Rector Magnificus prof. dr. J.H.J.M van Krieken,  
according to the decision of the Council of Deans  
to be defended in public on Tuesday, November 12, 2019  
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# 1. Introduction

Feeding Barn swallow *Hirundo rustica*. Photo credit: Jouke Altenburg

Caspar A. Hallmann

## 1.1 Background

We live in an era of biodiversity crisis. An era that is characterized by an accelerated rate of biodiversity loss, with some research suggesting we are in the midst of the sixth mass extinction (Ceballos *et al.*, 2015), marking a transition from the Holocene to the Anthropocene (Dirzo *et al.*, 2014). Besides the intrinsic value of biodiversity as prime justification for its preservation, loss of biodiversity is bound to have consequences for human well-being, through effects on ecosystem services, stability of ecosystem functioning, effects on economy, and so forth. These potentially devastating effects have provoked the need to establish the extent of biodiversity loss, as well as to uncover the determinants thereof. The premise being that knowledge of the causes and mechanisms involved is key to developing mitigation measures, and to halt and reverse population declines as well as to prevent species extirpation.

The major global threats to biodiversity identified are habitat destruction, agricultural intensification, overexploitation of natural resources, and increasingly climate change and invasive species (WWF International, 2016, 2018; IPBES, 2019). Agricultural intensification however, is currently accounting for the largest part of biodiversity loss (WWF International, 2016, 2018), particularly so in the more developed countries such as the Netherlands. Among birds in Europe for example, congruent patterns reveal farmland birds are in severe decline (Chamberlain & Fuller, 2000; Inger *et al.*, 2015; Gregory *et al.*, 2019), more than forest, wetland or shore birds, and more so where agricultural intensity is highest (Gregory *et al.*, 2005). Similar observations have been made for invertebrates such as butterflies (Kuussaari *et al.*, 2007; van Swaay *et al.*, 2013; Habel *et al.*, 2016; Thomas, 2016) and moths (Conrad *et al.*, 2006; Fox *et al.*, 2014). Aspects of modern agriculture have also been implicated in the alarming global decline of wild and domesticated pollina-

tors (Geiger *et al.*, 2010; Potts *et al.*, 2010; Goulson, 2013; Gilburn *et al.*, 2015). However, where arthropod diversity and abundance is clearly lowered in modern agricultural settings in Europe (Benton *et al.*, 2002; Geiger *et al.*, 2010; Habel *et al.*, 2019c), assessing the state of insects is generally hampered by lack of appropriate data at large spatial and temporal scales. Where data do exist, inference is generally restricted to a few well-known indicator taxa such as butterflies (Warren *et al.*, 2001; Kuussaari *et al.*, 2007; Van Dyck *et al.*, 2009; van Swaay *et al.*, 2013; Habel *et al.*, 2016), moths (Conrad *et al.*, 2006; Fox *et al.*, 2014) and wild bees (Goulson *et al.*, 2008), limiting the generalizations that can be made for insect communities as a whole, and more importantly, prohibiting assessment of the effects of various drivers (e.g. pesticides, climate change) on insects. For example, among approximately 20,000 insect species in the Netherlands, reliable country wide information on long-term trends exist only for butterflies and dragonflies (Kleijn *et al.*, 2018, [www.clo.nl](http://www.clo.nl)).

## 1.2 Farmland biodiversity is under severe threat

Agricultural intensification in Europe has manifested itself through a broad homogenization and simplification of the landscape (Tschardt *et al.*, 2005). Modern high-intensity land-use systems such as in the Netherlands are characterized by little non-crop habitat, little crop diversity, little structural heterogeneity, and by a high intensity and a high frequency of agronomic practices. Approximately 60% of the surface in the Netherlands is nowadays devoted to agriculture (CBS, 2018a), forming one of the most intensively used landscapes in the world.

Effects of agricultural intensification on biodiversity include habitat loss, habitat fragmentation and habitat deterioration. Conversion of land for agriculture and urban expansion, loss of semi-natural areas (e.g. field margins, corridors along watercourses, hedgerows), increased harvesting frequencies (e.g. in grasslands), drainage of the land, and high livestock densities have turned many areas unsuitable to support a range of species traditionally found in farmland (Donald *et al.*, 2001; Vickery *et al.*, 2001). Increased isolation of natural and semi-natural areas in between the agricultural and urban landscape, have reduced connectivity of less mobile and more specialized species, and as a rule, these species have been more prone to stochastic extirpation. This has led to a large-scale homogenization of invertebrate (Carvalho *et al.*, 2013), plant (Carvalho *et al.*, 2013) and avian (van Turnhout *et al.*, 2010) communities, with common, widespread generalist species usually dominating each group.

Among aspects of agricultural intensification, large-scale pesticide as well as synthetic fertilizers application is widely considered to be major contributors to biodiversity declines in farmland (Donald *et al.*, 2001; Benton *et al.*, 2002; Boatman *et al.*, 2004; Geiger *et al.*, 2010; Nijssen *et al.*, 2017; WallisDeVries & Bobbink, 2017). Organisms living within the agricultural landscape may find themselves exposed to agrochemicals, and/or may be affected indirectly through a lowering of habitat quality (Potts, 1986; Newton, 2004). Insecticides for example have been shown in the past to be able to accumulate in the food chain, and to affect species at multiple trophic levels (Carson, 1962; Opdam *et al.*, 1987), showing that the adverse effects need not be limited to impacts on single species only, but may cause disruptions of ecosystem functions (e.g. Schäfer *et al.*, 2007). Also recently, application of pesticides in farmlands have been linked to declines of both arthropod and

avian communities (Benton *et al.*, 2002; Boatman *et al.*, 2004; Newton, 2004; Geiger *et al.*, 2010; Mineau & Whiteside, 2013), and have also been implicated in the global declines of pollinators (Potts *et al.*, 2010), as well as the plants they pollinate (Biesmeijer *et al.*, 2006).

Growing resistance of certain pest species towards plant protection products, as well as concerns amid environmental risks posed by older generations of pesticides, have led to the development and introduction of new generations of insecticides, such as the neonicotinoids. The application of neonicotinoids have recently been heavily debated, as these insecticides have been implicated in the global declines of pollinators (Potts *et al.*, 2010; Pisa *et al.*, 2015), and are generally thought to pose serious environmental risk (Goulson, 2013; Gibbons *et al.*, 2015; Zeng *et al.*, 2013; Chagnon *et al.*, 2015; Botías *et al.*, 2016; Wood & Goulson, 2017). Usage in the Netherlands has been profound up to now, with for example the amount of neonicotinoids among other insecticides, accounting for a 16% share (21.429 kg active ingredient) of the total amount of insecticides in 2016 (Nefyto, 2017). Contamination in waterways has been reported in the Netherlands (Dutch Pesticides Atlas, 2009) and elsewhere (Morrissey *et al.*, 2015; Stehle & Schulz, 2015), suggesting they can leach into non-target environments, including natural and semi-natural areas. In experimental settings, neonicotinoids have been found to be highly toxic at very low concentrations to many non-target species (Easton & Goulson, 2013; Roessink *et al.*, 2013), while empirically, they have been linked to severely reduced arthropod abundances in contaminated surface water in the Netherlands (van Dijk *et al.*, 2013), declines in butterflies in the UK (Gilburn *et al.*, 2015), and declines of wild bees in Sweden (Rundlöf *et al.*, 2015). Furthermore, the effect of neonicotinoids, being selective towards invertebrates, were thought to be minimal to birds and mammals, as they target neurological processes specific to insects only (Matsuda *et al.*, 2001, but see Chapter 6). Regardless of the validity of this presumption, indirect effects of neonicotinoids on species higher in the trophic chain may exist, for example through lowering of a prey base for predators, however, this has not been tested up to date.

### 1.3 Research outline

The above introduction points to several gaps in knowledge on the current threats to farmland biodiversity. Given that neonicotinoids are comparatively very toxic to insects, are widely used, and are prone to leaching into the environment, the question emerges whether application of such insecticides can affect wildlife -beyond that of pest species- in the natural environment. In particular, this dissertation therefore addresses the following two research questions:

1. Are insectivorous bird population dynamics related to neonicotinoid pesticide contamination near farmland areas?
2. What is the state of insects as a whole in modern agriculture-dominated landscapes?

Below I introduce the two research questions and set out the research objectives of this thesis.

### 1.4 Neonicotinoids and farmland birds

As one of the core questions in the dissertation, in **Chapter 2**, we hypothesize that a recently introduced insecticide, imidacloprid, spatially and temporally correlates with

local insectivorous bird trends. In addition, we compare the impact of imidacloprid loads in surface waters on bird trends to those of land use changes in the same period. The results from this exercise suggest that the consequences of environmental contamination by neonicotinoids to be more severe than had been anticipated before. Although correlative, our findings suggest a negative impact of neonicotinoids on the trends of common bird species in farmland, a correlation that could not be attributed to other changes in the agricultural landscape. This leads to the hypothesis that in areas with neonicotinoid contamination, insect stocks have been affected to the extent that they are causing a food shortage for higher trophic levels.

## 1.5 The state of insects in Germany and Netherlands

Insects are a crucial and indispensable component of ecosystems. Their sheer diversity and abundance are indicative to the many ecosystem functions they fulfill, and as (Wilson, 1987) has stated, they are *the little things that run the world*. Given the observation of spatially variable trends of insectivorous birds in the Netherlands (Chapter 2) as well as broad declines in insectivorous birds elsewhere (Vickery *et al.*, 2001; Hladik & Kolpin, 2016; Bowler *et al.*, 2019; Møller, 2019), one may ask to what extent are insects still able to maintain healthy populations in human-dominated landscapes. In **Chapter 3**, we therefore assess the state of flying insects in German lowland nature reserves, and investigate a number of possible drivers as possible culprits in the insect decline. We demonstrate a severe decline in total flying insect biomass across ecosystem types, and a decline that cannot be explained by a number of potentially driving factors. The results suggest that insect biomass in nature reserves have been to a large extent decimated, with declines of sufficient magnitude to be expected to disrupt a large number of ecosystem processes such as pollination, energy flow and nutrient cycling.

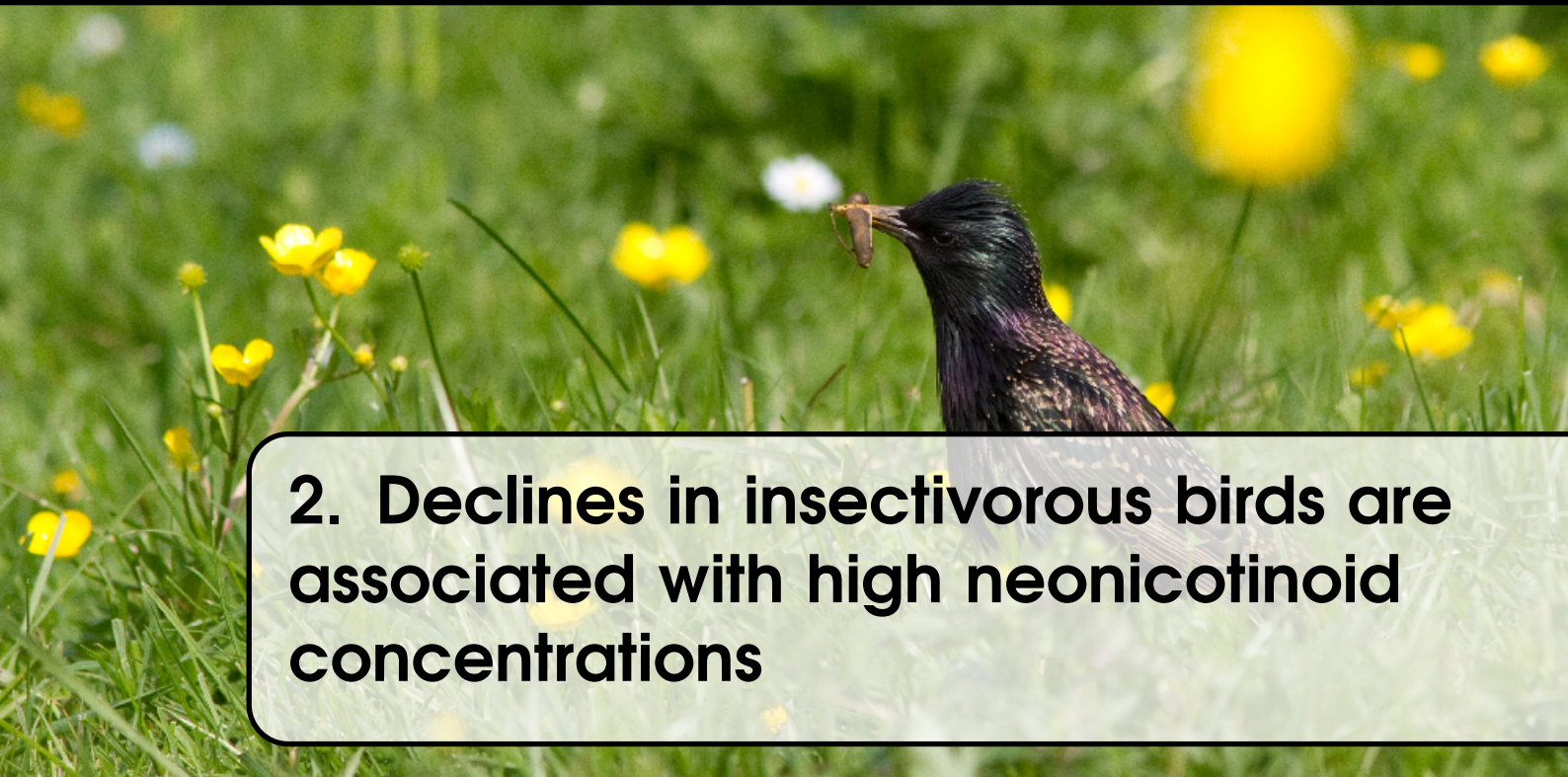
The observation of severe insect declines in Germany has sparked concerns for the state of insects elsewhere (Sánchez-Bayo & Wyckhuys, 2019), and hence the need to evaluate the geographic extent of the decline, as well as its consequence for biodiversity. Because the type, size and surrounding landscape structure of nature reserves in Germany and the Netherlands share many common features, insect declines may also occur in similar landscapes in the Netherlands, an extrapolation that obviously needs to be investigated. In **Chapter 4** we therefore assess the state of entomofauna in the Netherlands in a number of well-managed nature reserves, and across a number of insect orders (Coleoptera, macro-Lepidoptera, Trichoptera, Ephemeroptera, Neuroptera and Hemiptera). Findings of this study largely confirm the expectation that the insects in the Netherlands are under severe pressure as well, although trends vary considerably between the different insect orders examined.

A decline in biomass of flying insects may reflect species loss, a decline in abundance, a change in the weight distribution of the species, or any combination of those. The consequences for pollination, food supply and other ecological functions will critically depend on these relationships. To investigate how well insect biomass declines reflect biodiversity decline, in **Chapter 5** we assess how trends in flying insect biomass related to trends in richness, abundance and diversity of hoverfly (*Syrphidae*) species. As hoverflies are a highly diverse family of insects, they have often been promoted as suitable indicators of ecosystem health (Sommaggio, 1999). Examination of trends in abundance of hoverflies

may therefore help in elucidating the nature of insect declines.

In **Chapter 6**, I summarize the outcomes of this thesis and synthesize with existing knowledge of the state of biodiversity in modern agricultural landscapes. Additionally, I discuss the possible role of large-scale pesticide application on biodiversity loss and I conclude by identifying a number of pertinent research priorities for biodiversity conservation in modern agricultural landscapes.





## 2. Declines in insectivorous birds are associated with high neonicotinoid concentrations

Foraging Common starling *Sturnus vulgaris*. Photo credit: Jouke Altenburg

Hallmann, C. A., Foppen, R. P., van Turnhout, C. A., de Kroon, H., & Jongejans, E. (2014). Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature*, **511**, 341–343.

### Abstract

Recent studies have shown that neonicotinoid insecticides have adverse effects on non-target invertebrate species. Invertebrates constitute a substantial part of the diet of many bird species during the breeding season and are indispensable for raising offspring. We investigated the hypothesis that the most widely used neonicotinoid insecticide, imidacloprid, has a negative impact on insectivorous bird populations. Here we show that, in the Netherlands, local population trends were significantly more negative in areas with higher surface-water concentrations of imidacloprid. At imidacloprid concentrations of more than 20 nanograms per liter, bird populations tended to decline by 3.5 per cent on average annually. Additional analyses revealed that this spatial pattern of decline appeared only after the introduction of imidacloprid to the Netherlands, in the mid-1990s. We further show that the recent negative relationship remains after correcting for spatial differences in land-use changes that are known to affect bird populations in farmland. Our results suggest that the impact of neonicotinoids on the natural environment is even more substantial than has recently been reported and is reminiscent of the effects of persistent insecticides in the past. Future legislation should take into account the potential cascading effects of neonicotinoids on ecosystems.



## 2.1 Introduction

Although concerns have been raised about the direct effects of neonicotinoids on non-target vertebrate species (Goulson, 2013), neonicotinoids are in general thought to be less harmful to mammals and birds than to insects. The main mode of action of neonicotinoids occurs through binding nicotinic acetylcholine receptors in the central nervous system of invertebrates (Matsuda *et al.*, 2001), and neonicotinoids bind with substantially less affinity to these receptors in vertebrates (Tomizawa & Casida, 2005). This property has made neonicotinoids highly favoured agrochemicals worldwide over the past two decades (Pollak, 2011). In the Netherlands, imidacloprid was first administered by the Board for the Authorisation of Plant Protection Products and Biocides (Ctgb) in August 1994. Annual use increased rapidly from 668 kg in 1995 to 5,473 kg in 2000 and 6,332 kg in 2004 (Statistics Netherlands, 2013). Since 2003, imidacloprid has ranked consistently in the top three pesticides that exceed the environmental concentrations permitted by quality standards in the Netherlands (Dutch Pesticides Atlas, 2009; van Dijk *et al.*, 2013).

As neonicotinoids have relatively long half-lives in soil and are water soluble, they have the potential to accumulate in soils and to leach into surface water and ground water. Their systemic property (that is, their ability to spread through all of the tissues of the plants under treatment), together with their widespread use, indicates that many organisms in agricultural environments are likely to become exposed (Goulson, 2013). Indeed, studies have shown, both in experimental and in field conditions, that neonicotinoids may affect non-target invertebrate species across terrestrial and aquatic ecosystems (Easton & Goulson, 2013; Roessink *et al.*, 2013; van Dijk *et al.*, 2013). The question remains, however, whether the effects are sufficiently severe to affect ecosystems through trophic interactions: that is, beyond the direct lethal and sublethal effects on individual species. In the past, the introduction of insecticides has caused prey-base collapses, which in turn affected avian populations (Newton, 1998; Boatman *et al.*, 2004; Poulin *et al.*, 2010), showing that pesticide-induced declines in invertebrate densities can cause food deprivation for birds. Thus, if natural insect communities are indeed affected by neonicotinoids to the extent of causing disruptions in the food chain, we may expect insectivorous bird species to be affected as well.

The present study takes advantage of two standardized, long-term, country-wide monitoring schemes in the Netherlands (see Methods)-the Dutch Common Breeding Bird Monitoring Scheme (van Turnhout *et al.*, 2010) and surface-water quality measurements (van Dijk *et al.*, 2013) to investigate the extent to which average concentrations of imidacloprid residues in the period 2003–2009 spatially correlate with bird population trends in the period 2003–2010. We selected 15 passerine species that are common in farmlands and depend on invertebrates during the breeding season (Supplementary Table A1 and Supplementary Methods). We interpolated concentrations of imidacloprid in surface water to bird monitoring plots (Appendix A: Supplementary Figures A1,A2,A3, Supplementary Data and Supplementary Methods) and examined how local bird trends correlate with these concentrations (Figure 2.1a).

## 2.2 Results and Discussion

The average intrinsic rate of increase in local farmland bird populations was negatively affected by the concentration of imidacloprid (Figure 2.1b, linear mixed effects regres-

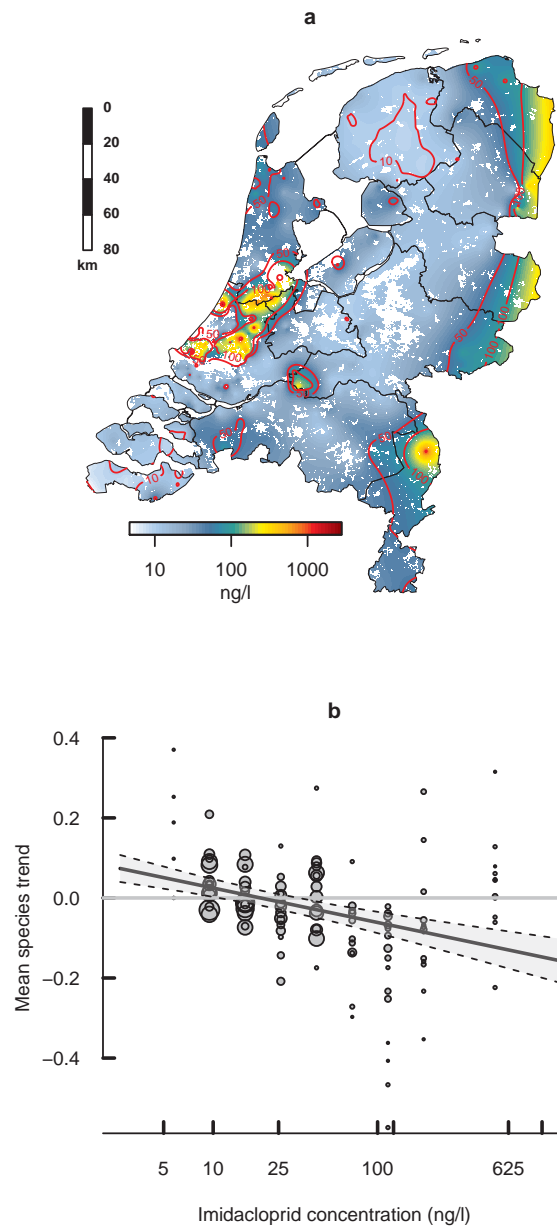


Figure 2.1: **Effects of imidacloprid on bird trends in the Netherlands.** **a**, Interpolated (universal kriging) mean log-concentrations of imidacloprid in the Netherlands (2003-2009). **b**, Relationship between average annual intrinsic rate of increase over 15 passerine birds and imidacloprid concentrations in Dutch surface water. Each point represents the average intrinsic rate of increase of a species over all plots in the same concentration class, while the size of the point is scaled proportionally to the number of species-plot combinations on which the calculated mean is based. Binning into classes was performed to reduce scatter noise and aid visual interpretation. Actual analysis and depicted regression line were performed on raw data ( $n=1459$ ). Regression line given by:  $0.1110-0.0374(\text{se}=0.0066) * \log(\text{imidacloprid})$  ( $P<0.0001$ ).

sion (LMER): d.f. = 1,443,  $t = -5.64$ ,  $P < 0.0001$ ). At the separately tested individual species level, 14 out of 15 of the tested species had a negative response to interpolated imidacloprid concentrations, and 6 out of 15 had a significant negative response at the 95% confidence level after Bonferroni correction (Table 2.1 and Supplementary Figure A4). Thus, higher concentrations of imidacloprid in surface water in the Netherlands are consistently associated with lower or negative population growth rates of passerine insectivorous bird populations. From our analysis, the imidacloprid concentration above which bird populations were in decline was  $19.43 \pm 0.03$  ng l<sup>-1</sup> (mean  $\pm$  s.e.m.) (Figure 2.1b). In areas with imidacloprid measurements above this concentration, bird populations declined by 3.5% on average annually.

**Table 2.1: Effects of imidacloprid concentrations on annual intrinsic rate of increase for individual insectivorous bird species.** Species with significant imidacloprid effects after Bonferroni correction are indicated with an asterisk.

| Species   | Effect  | se     | t-value | P       | n   |
|---|---------|--------|---------|---------|-----|
| Marsh warbler ( <i>Acrocephalus palustris</i> )     | 0.0110  | 0.0187 | 0.5871  | 0.5584  | 105 |
| Sedge warbler ( <i>Acrocephalus schoenobaenus</i> ) | -0.0229 | 0.0152 | -1.5070 | 0.1351  | 99  |
| Reed warbler ( <i>Acrocephalus scirpaceus</i> )     | -0.0348 | 0.0145 | -2.3949 | 0.0180  | 138 |
| Eurasian skylark ( <i>Alauda arvensis</i> )         | -0.0684 | 0.0189 | -3.6164 | 0.0004* | 125 |
| Meadow pipit ( <i>Anthus pratensis</i> )            | -0.0299 | 0.0184 | -1.6273 | 0.1053  | 200 |
| Yellowhammer ( <i>Emberiza citrinella</i> )         | -0.0385 | 0.0179 | -2.1578 | 0.0367  | 44  |
| Icterine Warbler ( <i>Hippolais icterina</i> )      | -0.0705 | 0.0313 | -2.2501 | 0.0285  | 57  |
| Barn swallow ( <i>Hirundo rustica</i> )             | -0.2313 | 0.0544 | -4.2540 | 0.0007* | 17  |
| Yellow wagtail ( <i>Motacilla flava</i> )           | -0.1255 | 0.0272 | -4.6145 | 0.0000* | 124 |
| Tree sparrow ( <i>Passer montanus</i> )             | -0.1301 | 0.0815 | -1.5971 | 0.1211  | 31  |
| Willow Warbler ( <i>Phylloscopus trochilus</i> )    | -0.0036 | 0.0094 | -0.3827 | 0.7025  | 154 |
| Stonechat ( <i>Saxicola rubicola</i> )              | -0.0279 | 0.0211 | -1.3241 | 0.1891  | 85  |
| Common starling ( <i>Sturnus vulgaris</i> )         | -0.1070 | 0.0315 | -3.3991 | 0.0013* | 57  |
| Common whitethroat ( <i>Sylvia communis</i> )       | -0.0408 | 0.0125 | -3.2751 | 0.0013* | 179 |
| Mistle thrush ( <i>Turdus viscivorus</i> )          | -0.1093 | 0.0277 | -3.9480 | 0.0003* | 44  |

We checked whether two alternative explanations could have caused spurious correlations between imidacloprid concentrations and bird population trends over the period 2003–2010. First, it is possible that our results could simply reflect a spatial pattern of local farmland bird declines that started before the introduction of imidacloprid (van Turnhout *et al.*, 2007). Therefore, we tested whether declines were present before the introduction of imidacloprid, in 1994. In contrast to the strongly negative relationship between imidacloprid concentration and bird population trends in 2003–2010 (Figure 2.1b), the 2003–2009 imidacloprid concentrations were not significantly associated with bird trends in the period 1984–1995 ( $t = -1.43$ ,  $P = 0.15$  for LMER<1995;  $t = -2.16$ ,  $P = 0.031$  for LMER>2003; using plots only with trend data for both periods, d.f. = 365; see Appendix A: Supplementary Figure A6 and Supplementary Methods). Overall, bird population trends in these two periods, paired by plot and species, were uncorrelated ( $r = -0.028$ , Pearson product moment test;  $t = -0.5455$ , d.f. = 379,  $P = 0.56$ ). We can thus conclude that the spatial pattern observed does not reflect long-term ongoing local declines caused by other factors. This finding suggests that imidacloprid is likely to have

contributed to the declining population trend of the local birds.

Second, we tested whether spatial differences in land-use changes related to agricultural intensification confounded the effects of imidacloprid in our analyses. We performed multiple mixed effects regression analyses in which we included the local changes in land area use (urban area, natural area, and the production areas of maize, winter cereals and fallow land) and the amount of fertilizer applied (nitrogen in kg ha<sup>-1</sup>) as fixed explanatory variables (see Appendix A: Supplementary Data), in addition to imidacloprid concentrations. These variables have been put forward frequently as causal factors related to farmland bird declines (Newton, 2004; Chamberlain & Fuller, 2000; Fuller, 2000), although their major effect may have already occurred earlier in the twentieth century. As imidacloprid usage is likely to be related to horticulture and greenhouses (van Dijk *et al.*, 2013), spatial changes in these variables may confound the effects of imidacloprid on bird trends. We therefore also incorporated changes in the area of greenhouses and the area of flower bulb production in our analysis. The results indicate that the concentration of imidacloprid and the changes in urban and natural areas were negatively correlated with local population trends, whereas the changes in the bulb and fallow land were positively correlated (Figure 2.2). However, only imidacloprid and bulb area were significantly correlated with local trends (Supplementary Table A2).

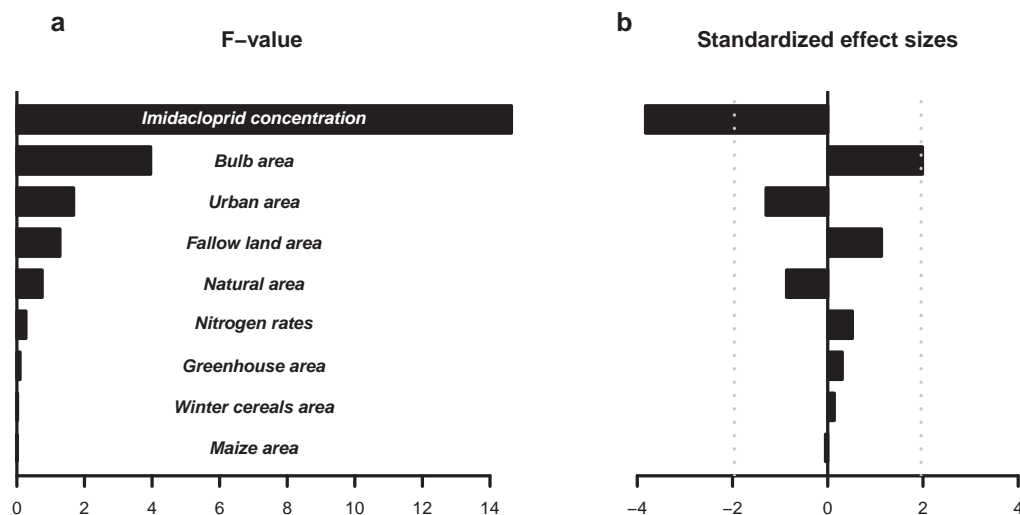


Figure 2.2: **Comparison of the effects of agricultural land-use changes versus the effects of imidacloprid on bird population trends.** **a**, Marginal variance ratio (F) of each effect estimated from a mixed effects model with all species data pooled. **b**, Standardized effect sizes ( $t$ -values) for each covariate from the mixed-effects model. Vertical dotted lines represent significance thresholds at  $\alpha=0.05$  (2-sided). Imidacloprid concentrations and proportional changes in bulb-production areas were the only variables that had significantly negative effects (LMER:  $df=1349$ ,  $t=-3.825$ ,  $P=0.0001$  for imidacloprid and  $t=1.989$ ,  $P=0.0468$  for bulbs).

So far, the suggested potential risks of neonicotinoids for birds have focused on the acute toxic effects caused by direct consumption (Goulson, 2013). Our results suggest another possibility: that is, that the depletion of insect food resources has caused the observed relationships. Two lines of evidence seem to support this. First, 9 out of 15 species tested in the present study are exclusively insectivorous. All 15 species feed their young (almost) exclusively with invertebrates, and food demand is the highest in this period. Adult skylarks, tree sparrows, common starlings, yellowhammers, meadow pipits and mistle thrushes are also granivorous to some extent and may thus directly consume coated seed. However, meadow pipits and mistle thrushes forage on seeds only outside the breeding season, and for all 15 species the bulk of the diet during the breeding season consists of invertebrates (Cramp & Perrins, 1994). Second, recent *in situ* research involving the same areas as the present study revealed strong declines in insect macrofauna, including species that have a larval stage in water, where imidacloprid concentrations were elevated (van Dijk *et al.*, 2013). These insects (particularly Diptera, Ephemeroptera, Odonata, Coleoptera and Hemiptera) are an important food source in the breeding season for the bird species that we investigated (Cramp & Perrins, 1994). However, as our results are correlative, we cannot exclude other trophic or direct ways in which imidacloprid may have an effect on the bird population trends. Food resource depletion may not be the only or even the most important cause of decline. Other possible causes of decline include trophic accumulation of this neonicotinoid through consumption of contaminated invertebrates and, for the six partly granivorous species involved, sublethal or lethal effects through the ingestion of coated seeds (Goulson, 2013). The relative effect sizes of these pathways urgently need to be investigated.

Farmland birds have experienced tremendous population declines in Europe in the past three decades, with agricultural intensification as the primary causal factor (Chamberlain & Fuller, 2000; Fuller, 2000; Newton, 2004; Gregory *et al.*, 2005). Among aspects of intensification, pesticides are known to be a major threat to farmland birds (Boatman *et al.*, 2004; Geiger *et al.*, 2010; Mineau & Whiteside, 2013). Neonicotinoids have recently replaced older intensively used insecticides such as carbamates, pyrethroids and organophosphates. After neonicotinoids were introduced to the Netherlands in the mid-1990s, their application was intensified, and the concentrations found in the environment frequently exceeded environmental standards, despite these concentrations being shown to have severe detrimental effects on several insect communities. Our results on the declines in bird populations suggest that neonicotinoids pose an even greater risk than has been anticipated. Cascading trophic effects deserve more attention in research on the ecosystem effects of this class of insecticides and must be taken into account in future legislation.

## 2.3 Methods

### 2.3.1 Data

We derived population trends for 15 insectivorous farmland passerine species (see Appendix A: Supplementary Data, Supplementary Methods and Supplementary Table A1 for the list of species) using long-term breeding bird data from the Dutch Common Breeding Bird Monitoring Scheme, a standardized (Bibby *et al.*, 1992; van Dijk, 2004) monitoring scheme maintained and coordinated by Sovon, Dutch Centre for Field Ornithology, in collaboration with Statistics Netherlands (van Turnhout *et al.*, 2010). The scheme has

been running in the Netherlands since 1984. Data originating from these monitoring plots are generally considered to be adequately representative and reliable for population trend estimation (van Turnhout *et al.*, 2010, 2007; Bibby *et al.*, 1992; Devictor *et al.*, 2012; Kampichler *et al.*, 2012). The monitoring plots are well scattered throughout the Netherlands and range in size between 10 ha and 1,000 ha (Supplementary Figure A2).

We used previously described information on imidacloprid concentrations in Dutch surface water (van Dijk *et al.*, 2013). This data set was collected by the Dutch waterboard authorities as part of the regular monitoring of surface-water pesticide contamination (Dutch Pesticides Atlas, 2009) (see Supplementary Data for details). Imidacloprid concentration measurements throughout the Netherlands are available (Supplementary Figure A1); hence, this data set is considered an adequate representation of the actual water contamination levels in the Netherlands. The geographical locations of the two monitoring programs do not generally spatially coincide. To combine the data sets, we interpolated imidacloprid concentrations from water quality measurement locations to bird monitoring plots (see Appendix A: Supplementary Data).


### 2.3.2 Statistical analysis

To assess the overall effects of expected concentrations on all species simultaneously, we used linear mixed effects models with species- and plot-specific population trends (intrinsic rates of increase or  $\log[\lambda]$ ) as the response,  $\log$ [concentration of (interpolated) imidacloprid] as the fixed explanatory variable and species as a random factor. Additionally, we performed linear regressions of the population trends against the logarithm of the imidacloprid concentrations for each species separately using weighted least squares. The trends per plot were weighted by the mean species population size of the plot, to avoid the large influence of the demographic stochasticity of small populations. Population trends were calculated as the slope of  $\log$ [territory counts] versus year of sampling (that is, a continuous trend) (see Supplementary Data). Regressions were performed using all monitoring plots located less than 5 km between the edge of a plot and an imidacloprid measurement location. This cut-off point of 5 km balanced the preferable proximity between bird and imidacloprid measurements with the amount of data retained in the analyses. However, regardless of how we varied the cut-off value between 1 and 25 km (that is, including between 7% and 99% of the bird monitoring plots, respectively), the effect size of imidacloprid on bird population trends remained strongly significantly negative (see Appendix A: Supplementary Methods and Supplementary Figure A5). We examined potential confounding of the spatial imidacloprid concentrations with several different candidate explanatory variables that have been postulated as possible causes of farmland bird declines<sup>19</sup> and that are relevant to the Netherlands (van Turnhout *et al.*, 2010). We used eight variables (Statistics Netherlands, 2013) that are potentially confounded with the introduction of imidacloprid: namely, proportional change in the area of maize, proportional change in winter cereal cropping area, proportional change in flower bulb area, change in the amount of fertilizer application (nitrogen in kg ha<sup>-1</sup>), proportional change in greenhouse area, proportional change in urban area, proportional change in natural habitat area and proportional change in fallow land area (Appendix A: Supplementary Data). We compared the significance of all explanatory variables using a multiple mixed effects model (with species intercept as a random effect) paired with F tests based on single term deletions of the full model (Figure 2.2a). In addition, we compared standardized effect

sizes (coefficient/s.e.m.) between explanatory variables based on single species multiple linear regression models (Figure 2.2b and Appendix A: Supplementary Methods).

## **Acknowledgments**

We thank A. J. van Dijk, H. Sierdsema and D. Zoetebier for processing the bird data sets and J. P. van der Sluijs for sharing the database with imidacloprid concentration measurements. The Breeding Bird Monitoring Program is organised in close collaboration with Statistics Netherlands and provinces and is funded by the Dutch Ministry of EZ. We thank Sovon volunteers for their efforts in the field. The study was supported by NWO grants 840.11.001 and 841.11.007 and was the result of a collaboration within the Center for Avian Population Studies.



### 3. More than 75 percent decline over 27 years in total flying insect biomass in protected areas

Malaise trap in German nature reserve. Photo credit: *Martin Sorg*

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS one*, **12**(10), e0185809.

#### **Abstract**

Global declines in insects have sparked wide interest among scientists, politicians, and the general public. Loss of insect diversity and abundance is expected to provoke cascading effects on food webs and to jeopardize ecosystem services. Our understanding of the extent and underlying causes of this decline is based on the abundance of single species or taxonomic groups only, rather than changes in insect biomass which is more relevant for ecological functioning. Here, we used a standardized protocol to measure total insect biomass using Malaise traps, deployed over 27 years in 63 nature protection areas in Germany (96 unique location-year combinations) to infer on the status and trend of local entomofauna. Our analysis estimates a seasonal decline of 76%, and mid-summer decline of 82% in flying insect biomass over the 27 years of study. We show that this decline is apparent regardless of habitat type, while changes in weather, land use, and habitat characteristics cannot explain this overall decline. This yet unrecognized loss of insect biomass must be taken into account in evaluating declines in abundance of species depending on insects as a food source, and ecosystem functioning in the European landscape.



### 3.1 Introduction

Loss of insects is certain to have adverse effects on ecosystem functioning, as insects play a central role in a variety of processes, including pollination (Öckinger & Smith, 2007; Ollerton *et al.*, 2011), herbivory and detritivory (Mattson & Addy, 1975; Yang & Gratton, 2014), nutrient cycling (Yang & Gratton, 2014) and providing a food source for higher trophic levels such as birds, mammals and amphibians. For example, 80% of wild plants are estimated to depend on insects for pollination (Ollerton *et al.*, 2011), while 60% of birds rely on insects as a food source (Morse, D, 1971). The ecosystem services provided by wild insects have been estimated at \$57 billion annually in the USA (Losey & Vaughan, 2006). Clearly, preserving insect abundance and diversity should constitute a prime conservation priority.

Current data suggest an overall pattern of decline in insect diversity and abundance. For example, populations of European grassland butterflies are estimated to have declined by 50% in abundance between 1990 and 2011 (van Swaay *et al.*, 2013). Data for other well-studied taxa such as bees (Goulson *et al.*, 2008; Nilsson *et al.*, 2008; Winfree *et al.*, 2009; Potts *et al.*, 2010; Ilyinykh, 2011; Ollerton *et al.*, 2014; Woodcock *et al.*, 2016) and moths (Conrad *et al.*, 2002, 2006; Fox, 2013; Fox *et al.*, 2014) suggest the same trend. Climate change, habitat loss and fragmentation, and deterioration of habitat quality have been proposed as some of the prime suspects responsible for the decline (Brändle *et al.*, 2001; Benton *et al.*, 2002; Morecroft *et al.*, 2002; Biesmeijer *et al.*, 2006; Nilsson *et al.*, 2008; Winfree *et al.*, 2009; Potts *et al.*, 2010; Fox *et al.*, 2014; Ollerton *et al.*, 2014). However, the number of studies on insect trends with sufficient replication and spatial coverage are limited (Winfree *et al.*, 2009; Fuentes-Montemayor *et al.*, 2011; Dirzo *et al.*, 2014; Thomas, 2016) and restricted to certain well-studied taxa. Declines of individual species or taxa (e.g. (van Swaay *et al.*, 2013; Habel *et al.*, 2016)) may not reflect the general state of local entomofauna (Thomas *et al.*, 2004). The total insect biomass would then be a better metric for the status of insects as a group and its contribution to ecosystem functioning, but very few studies have monitored insect biomass over an extensive period of time (Shortall *et al.*, 2009). Hence, to what extent total insect biomass has declined, and the relative contribution of each proposed factor to the decline, remain unresolved yet highly relevant questions for ecosystem ecology and conservation.

Here, we investigate total aerial insect biomass between 1989 and 2016 across 96 unique location-year combinations in Germany, representative of Western European low-altitude nature protection areas embedded in a human-dominated landscape (Supplementary Figure B3). In all years we sampled insects throughout the season (March through October), based on a standardized sampling scheme using Malaise traps. We investigated rate of decline in insect biomass, and examined how factors such as weather, habitat and land use variables influenced the declines. Knowledge on the state of insect biomass, and its direction over time, are of broad importance to ecology and conservation, but historical data on insect biomass have been lacking. Our study makes a first step into filling this gap, and provides information that is vital for the assessment of biodiversity conservation and ecosystem health in agricultural landscapes.

## 3.2 Materials and Methods

### 3.2.1 Data

#### Biomass Data

Biomass data were collected and archived using a standardized protocol across 63 unique locations between 1989 and 2016 (resulting in 96 unique location-year combinations) by the Entomological Society Krefeld. The standardized protocol of collection has been originally designed with the idea of integrating quantitative aspects of insects in the status assessment of the protected areas, and to construct a long-term archive in order to preserve (identified and not-identified) specimens of local diversity for future studies. In the present study, we consider the total biomass of flying insects to assess the state of local entomofauna as a group.

All trap locations were situated in protected areas, but with varying protection status: 37 locations are within Natura2000 sites, seven locations within designated Nature reserves, nine locations within Protected Landscape Areas (with funded conservation measures), six locations within Water Protection Zones, and four locations of protected habitat managed by Regional Associations. For all location permits have been obtained by the relevant authorities, as listed in the Supplementary Information 6.3. In our data, traps located in nutrient-poor heathlands, sandy grasslands, and dune habitats provide lower quantities of biomass as compared to nutrient rich grasslands, margins and wastelands. As we were interested in whether the declines interact with local productivity, traps locations were pooled into 3 distinct habitat clusters, namely: nutrient-poor heathlands, sandy grassland, and dunes (habitat cluster 1,  $n=19$  locations, Figure 3.1A), nutrient-rich grasslands, margins and wasteland (habitat cluster 2,  $n=41$  locations, Figure 3.1B) and a third habitat cluster that included pioneer and shrub communities ( $n=3$  locations).

Most locations (59%,  $n=37$ ) were sampled in only one year, 20 locations in two years, five locations in three years, and one in four years, yielding in total 96 unique location-year combinations of measurements of seasonal total flying insect biomass. Our data do not represent longitudinal records at single sites, suitable to derive location specific trends (e.g. (Shortall *et al.*, 2009)). Prolonged trapping across years is in the present context (protected areas) deemed undesirable, as the sampling process itself can negatively impact local insect stocks. However, the data do permit an analysis at a higher spatial level, i.e. by treating seasonal insect biomass profiles as 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 continuously (day and night), and catches were emptied at regular intervals, on average every 11.2 days ( $sd=6.3$ ). We collected in total 1503 trap samples, with an average of 16 (4-35) successive catches per location-year combination (Table 3.1). Between 1989 and 2016, a total of 53.54kg of invertebrates have been collected and stored, over a total trap exposure period of 16908 days, within an average of 176 exposure days per location-year combination. Malaise traps are known to collect a much wider diversity of insect species (e.g. (Bosch *et al.*, 1994; Schmidt & Robert, 1995; Hellenthal & Ssymank, 2007)) as compared to suction traps (e.g. (Shortall *et al.*, 2009)) and are therefore considered superior as a method of collecting flying insects. On the basis of partial assessments, we can assume that the total number of insects included in 53.54 kg biomass represents millions of individuals.

The sampling was standardized in terms of trap construction, size and design (identical

Table 3.1: **Overview of Malaise-trap samples sizes.** For each year, the number of locations sampled, the number of location re-sampled, total number of samples, as well as mean and standard deviation of exposure time at the trap locations (in days) are presented.

| Year | Number of locations | Number of locations sampled previously | Number of Samples | Mean exposure time | St. Dev exposure time |
|------|---------------------|--|-------------------|--------------------|-----------------------|
| 1989 | 8                   | 0                                      | 162               | 146.62             | 12.81                 |
| 1990 | 2                   | 0                                      | 62                | 228.50             | 34.65                 |
| 1991 | 1                   | 0                                      | 10                | 146.00             |                       |
| 1992 | 4                   | 0                                      | 54                | 118.75             | 15.50                 |
| 1993 | 4                   | 0                                      | 39                | 109.50             | 59.74                 |
| 1994 | 4                   | 0                                      | 60                | 170.75             | 72.83                 |
| 1995 | 2                   | 0                                      | 41                | 144.00             | 93.34                 |
| 1997 | 1                   | 0                                      | 20                | 162.00             |                       |
| 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                | 198.75             | 30.53                 |
| 2006 | 2                   | 0                                      | 26                | 188.00             | 0.00                  |
| 2007 | 2                   | 0                                      | 15                | 192.00             | 0.00                  |
| 2008 | 2                   | 0                                      | 24                | 162.00             | 0.00                  |
| 2009 | 4                   | 0                                      | 23                | 120.50             | 2.89                  |
| 2010 | 2                   | 0                                      | 12                | 85.00              | 0.00                  |
| 2011 | 1                   | 0                                      | 4                 | 68.00              |                       |
| 2012 | 2                   | 0                                      | 23                | 158.50             | 4.95                  |
| 2013 | 8                   | 2                                      | 126               | 175.50             | 21.71                 |
| 2014 | 23                  | 19                                     | 348               | 212.74             | 11.21                 |
| 2015 | 1                   | 1                                      | 10                | 224.00             |                       |
| 2016 | 7                   | 7                                      | 62                | 190.86             | 12.56                 |

parts), colors, type of netting and ground sealing, trap orientation in the field as well as slope at the trap location. Hence none of the traps differed in any of these field aspects. Our trap model was similar to the bi-colored malaise trap model by Henry Townes (Townes, 1972; Matthews & Matthews, 1983). The traps, collecting design, and accompanying methods of biomass measurement as designed and applied by the Entomological Society Krefeld are described elsewhere (Schwan *et al.*, 1993; Sorg, 1990; Sorg *et al.*, 2013) and in Supplementary Information 6.3.

Trap catches were stored in 80% ethanol solution, prior to weighing, and total insect biomass of each catch (bottle) was obtained based on a standardized measurement protocol by first subtracting fluid content. In order to optimally preserve samples for future species determination, the insects were weighed in an alcohol-wet state. First, the alcohol concentration in the vessels was stabilized to 80%, while this concentration was controlled with an areometer over a period of at least two days. In order to obtain biomass

per sample with sufficient accuracy and comparability, the measuring process was fixed using a standardized protocol (Schwan *et al.*, 1993). For this purpose the insects of a sample were poured onto a stainless steel sieve (10cm diameter) of 0.8 mm mesh width. This sieve is placed slightly obliquely (30 degrees) over a glass vessel. The skew position accelerates the first runoff of alcohol and thus the whole measuring procedure. The drop sequence is observed with a stopwatch. When the time between two drops has reached 10 seconds for the first time, the weighing process is performed with a laboratory scale. For the determination of the biomass, precision scales and analytical scales from Mettler company were used with an accuracy of at least 0.1g and controlled with calibrated test weights at the beginning of a new weighing series. In a series of 84 weightings of four different samples repeating this measurement procedure, an average deviation from the mean value of the measurement results of 0.4 percent was observed (unpublished results).

### Weather Data

Climate change is a well-known factor responsible for insect declines (Conrad *et al.*, 2002; Fliszkiewicz *et al.*, 2012; Fox *et al.*, 2014; Morecroft *et al.*, 2002). To test if weather variation could explain the observed decline, we included mean daily temperature, precipitation and wind speed in our analysis, integrating data from 169 weather stations (Deutscher Wetterdienst, 2015) located within 100km to the trap locations. We examined temporal trends in each weather variable over the course of the study period to assess changes in climatic conditions, as a plausible explanation for insect decline. Estimates of each weather variable at the trap locations were obtained by interpolation of each variable from the 169 climate stations.

We initially considered mean daily air temperature, precipitation, cloud cover, relative air moisture content, wind speed, and sunshine duration. However, only temperature, precipitation and wind speed were retained for analysis, as the other variables were significantly correlated with the selected variables [ $R(\text{temperature, cover})=-43.2\%$ ,  $R(\text{temperature, sunshine})=53.4\%$ ,  $R(\text{precipitation, moisture})=-47.3\%$ ] and because we wanted to keep the number of covariates as low as possible. Additionally, we calculated the number of frost days and the sum of precipitation in the months November- February preceding a sampling season. We used spatio-temporal geostatistical models (Cressie, 1993; Pebesma, 2004) to predict daily values for each weather variable to each trap location. Amongst other methods, the geostatistical approach is considered a superior interpolation method in order to derive weather variables to trap locations (Luo *et al.*, 2008). Uncertainty in interpolated variables such as wind speed is usually associated with altitude differences. However, as our trap locations are all situated in lowland areas with little altitude variation, we do not expect a large error in our interpolations at trap locations.

We decomposed the daily values of each weather variable into a long-term average trend (between years), a mean seasonal trend, and a yearly seasonal anomaly component (Supplementary Figure B4), modeled using regression splines (Wood, 2003) while controlling for altitude of weather stations. The remaining residual daily values of each station were further modeled using a spatio-temporal covariance structure. For example, temperature  $T$ , on given day  $t$ , of a given year  $k$  at a given trap location  $s$  is modeled as:

$$T(t, s, k) = f_k(k) + f_t(t) + r(k, t) + a \times h + C_{s,t} \quad (3.1)$$

where  $f_k(k)$  is the long-term trend over the years (a thin plate regression spline),  $f_t(t)$  the mean seasonal trend within years (a penalized cyclic cubic regression spline),  $r(k, t)$



Figure 3.1: Examples of operating malaise traps in protected areas in western Germany, in habitat cluster 1 (A) and cluster 2 (B) (see Materials and Methods).

the mean residual seasonal component, which measures annual anomaly in mean daily values across selected stations, and  $a$  is the linear coefficient for the altitude  $h$  effect. The spatio-temporal covariance structure  $C_{s,t}$ , fitted independently to the residuals of each weather variable model, allowed us to deal with lack of independence between daily weather data within and between stations, as well as to interpolate to trap locations using kriging. Altitude of trap locations was extracted from a digital elevation models at 90m resolution (Jarvis *et al.*, 2008).

### Land use Data

Land use variables (and changes therein) were derived from aerial photographs (TIM-online, 2016) taken within two distinct time periods (between 1989-1994, and between 2012-2015), and allowed us to characterize land use composition at surroundings of the traps, as well as changes over time. We distinguished cover of forests, agricultural areas, natural grassland, and surface water. For each trap location, aerial photographs were manually processed, polygons extracted and categorized, and their surface area calculated with a radius of 200 meter. Preliminary analysis of the relationship between log biomass and landuse variables, on a subset of the trap locations, indicated that land use elements at 200m radius better predicted insect biomass than elements at 500 and 1000m radius, similar to findings elsewhere for wild bees (Steffan-Dewenter *et al.*, 2002). Land use variables were measured at a coarse temporal resolution, but fortunately cover the temporal span of insect sampling. To link the cover of a given land use variable to the insect biomass samples in a particular year, we interpolated coverage between the two time points to the year of insect sampling using generalized linear models with a binomial error distribution, a logit link, and an estimated dispersion parameter. Mean distributions of land use at each of the two time points are depicted in Supplementary Figure B5.

### Habitat Data

Plant inventories were conducted in the immediate surroundings (within 50m) of the trap, in the same season of insect sampling. These data permitted the assessment of plant species richness (numbers of herbs, shrubs and trees) and environmental conditions based on average Ellenberg values (Ellenberg, 1974; Ellenberg *et al.*, 1992; Hennekens & Schaminée, 2001), as well as changes therein over time. Each Ellenberg indicator (we considered nitrogen, pH, light, temperature and moisture) was averaged over all species for each location-year combination. We examined annual trends in each of the above-mentioned variables in order to uncover potential structural changes in habitat characteristics over time. Species richness was analyzed using mixed-effects generalized linear models (Bates *et al.*, 2015) with a random intercept for trap location and assuming a Poisson distribution for species richness, and a normal distribution for mean Ellenberg indicator values. Although a Poisson distribution fitted tree and shrub species adequately, (residual deviance/ degree of freedom = 0.94 and 1.04 respectively), severe overdispersion was found for herb species richness (residual deviance/ degree of freedom = 2.16). Trend coefficients of richness over time between a Poisson mixed effects model and a negative binomial model were comparable but differed in magnitude (Poisson GLMM: -0.034 (se=0.003), vs NB GLMM -0.027 (se=0.006)). Although the fit is not perfect in the case of herb richness, we believe our trend adequately describes direction of change over time. Mean changes in plant species richness are depicted in Supplementary Figure B5C.

### 3.2.2 Insect Biomass Model

The temporal resolution of the trap samples (accumulated over several days) is not directly compatible with the temporal distribution of the weather data (daily values). Additionally, variable exposure intervals between trap samples is expected to induce variation in trapped biomass between samples, and hence induce heteroscedasticity. Furthermore, biomass data can numerically only be positive on the real line, and we require a model to reflect this property of the data. Because of the unequal exposure intervals however, log-transforming the response would be inappropriate, because we require the sum of daily values after exponentiation, rather than the exponent of the sum of log-daily biomass values. In order to indirectly relate biomass to daily weather variables, to account for the variation in time exposure intervals over which biomass was accumulated in the samples, and to respect the non-negative nature of our data, we modeled the biomass of each catch as the sum of the expected (but unobserved) latent daily biomass. The mass  $m$  of each sample  $j$ , at site  $s$  in year  $k$ , is assumed to be distributed normally about the sum of the latent expected daily mass ( $z_{t,s,k}$ ), with variance  $\sigma_j^2$ :

$$m_{j,s,k} \sim N(\mu_{j,s,k}, \sigma_j^2) \quad (3.2)$$

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

$$z_{t,s,k} = e^{y_{t,s,k}} \quad (3.3)$$

$$y_{t,s,k} = c + \log(\lambda)k + \mathbf{X}\beta_x + u_s \quad (3.4)$$

where  $c$  is a global intercept,  $\mathbf{X}$  a design matrix of dimensions  $n \times p$  (number of samples  $\times$  number of covariates; see Model analysis below),  $\beta_x$  the corresponding vector of coefficients that measure the weather, habitat and land use effects, and  $\log(\lambda)$  a mean annual population growth rate parameter. The random term ( $u_s$ ) denotes the location-specific random effect assumed to be distributed normally about zero  $u_s \sim N(0, \sigma_{site}^2)$ . The exponentiation of the right hand side of equation (3) ensures expected values to be positive.

The expected residual variance of each sample  $\sigma_j^2$ , is expressed as the sum of variances of daily biomass values ( $\sigma_{t,s,k}^2$ ).

$$\sigma_j^2 = \sum_{t=\tau_1(j)}^{\tau_2(j)} \sigma_{t,s,k}^2 \quad (3.5)$$

The variances of daily biomass should respect the non-negative nature of the data as well. Additionally, we are interested in being able to compare the residual variance with the random effects variance, and this requires them to be on the same scale. Therefore, we expressed the variance of the daily biomass as a function of the variance of the logarithm of the daily biomass. Using the method of moments:

$$\sigma_{t,s,k}^2 = e^{2y_{t,s,k} + v}(e^v - 1) \quad (3.6)$$

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

### 3.2.3 Analysis

We developed a series of models each consisting of a set of explanatory variables that measure aspects of climate, land use and local habitat characteristics. Significant explanatory variables in these models were combined into a final model, which was then reduced to exclude insignificant effects. An overview of which covariates were included in each model is given in Table 3.2.

Table 3.2: Overview of covariates included in each of the seven models. The year covariate yields the annual trend coefficient.

| Covariate class | Covariate name                 | Null model | Basic | Weather | Habitat | Land use | Land use+ Interactions | Final model |
|-----------------|--------------------------------|------------|-------|---------|---------|----------|------------------------|-------------|
| Temporal        | Intercept                      | ✓          | ✓     | ✓       | ✓       | ✓        | ✓                      | ✓           |
|                 | Day number                     | ✓          | ✓     | ✓       | ✓       | ✓        | ✓                      | ✓           |
|                 | Day number <sup>2</sup>        | ✓          | ✓     | ✓       | ✓       | ✓        | ✓                      | ✓           |
|                 | 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 <sup>2</sup> |            | ✓     | ✓       | ✓       | ✓        | ✓                      | ✓           |
|                 | Year × Agriculture             |            |       |         |         |          | ✓                      | ✓           |
|                 | Year × Forest                  |            |       |         |         |          | ✓                      | ✓           |
|                 | Year × Water                   |            |       |         |         |          | ✓                      | ✓           |
|                 | Year × Grassland               |            |       |         |         |          | ✓                      | ✓           |
| Variance        | $\sigma_{site}$                | ✓          | ✓     | ✓       | ✓       | ✓        | ✓                      | ✓           |
|                 | $\nu$                          | ✓          | ✓     | ✓       | ✓       | ✓        | ✓                      | ✓           |

Weather effects explored were daily temperature, precipitation and wind speed, as



well as the number of frost days and sum of precipitation in the preceding winter. Habitat effects explored tree and herb species richness, as well as average Ellenberg values for nitrogen, pH, light, temperature and moisture, per location-year combination. Land use effects explored the fractions of agricultural area, forest, grass, and surface water in a radius of 200m around the plot location.

Parameter values are obtained by the use of Markov chain Monte Carlo (MCMC) methods by the aid of JAGS (Just Another Gibbs Sampler (Plummer *et al.*, 2003)) invoked through R (R Core Team, 2015a) and the R2Jags package (Su & Yajima, 2015). JAGS model scripts and data are given in Appendix B: Supporting Information. For each model, we ran 3 parallel chains each consisting of 24000 iterations (first 4000 discarded), and kept every 10<sup>th</sup> value as a way to reduce within chain autocorrelation. We used vague priors for all parameters, with uniform distributions for the residual and random effect variance components, and flat normal distributions (with very high variance) for all other parameters. Covariates in **X** were standardized prior to model fitting, with the exception of year (values 1-26), and land use variables (proportions within 0-1 range).

For all models, we computed the Deviance Information Criterion (Spiegelhalter *et al.*, 2002) (DIC) as well as the squared correlation coefficient ( $R^2$ ) between observed and mean posterior estimates of biomass on the log scale. Results are given in Table 3.3. Parameter convergence was assessed by the potential scale reduction factor (Gelman & Rubin, 1992) (commonly  $\hat{R}$ ), that measures the ratio of posterior distributions between independent MCM chains (in all models, all parameters attained values below 1.02). For all models, we confirmed that the posterior distribution of the trend coefficient did not confound any other variable by plotting the relevant posterior samples and computing pairwise correlation coefficients.

Our basic model included habitat cluster (3 levels), a quadratic effect for day number, an annual trend coefficient measuring the rate of biomass change, and the interactions between the annual trend coefficient and the day number variables. Next we developed 3 models each consisting of either weather variables (Supplementary Table B1), land use variables (Supplementary Table B2), or habitat variables. Because interactions between the annual rate of change and land use variables seemed plausible, a fourth model was developed to include these interactions (Supplementary Table B3). Finally, all significant variables were combined into our final model (Table 3.4), which included effects of an annual trend coefficient, season (linear and quadratic effect of day number), weather (temperature, precipitation, number of frost days), land use (cover of grassland and water, as well as interaction between grassland cover and trend), and habitat (number of herb and tree species as well as Ellenberg temperature).

Our estimate of decline is based on our basic model, from which we can derive seasonal estimates of daily biomass for any given year. The basic model includes only a temporal (annual and seasonal effects, as well as interactions) and a basic habitat cluster distinction (additive effects only) as well as a random trap location effect. We here report the annual trend coefficient, as well as a weighted estimate of decline that accounts for the within season differences in biomass decline. The weighted insect biomass decline was estimated by projecting the seasonal biomass (1-April to 30-October) for years 1989 and 2016 using coefficients our basic model, and then dividing the summed (over the season) biomass of 2016 by the summed biomass over 1989.

Using our final model, we assessed the relative contribution (i.e. net effect) of the

explanatory variables to the observed decline, both combined and independently. To this aim we projected the seasonal daily biomass for the years 1989 and 2016 twice: first we kept covariates at their mean values during the early stages of the study period, and second we allowed covariate values to change according to the observed mean changes (see Supplementary Figures B4 and B5). Difference in the total biomass decline between these two projections are interpreted as the relative contribution of the explanatory variables to the decline. The marginal (i.e. independent) effects of each covariate were calculated by projecting biomass increase/decline as result of the observed temporal developments 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). As such, spatial variation in insect biomass may confound the estimated trend. To verify that this is not the case, we fitted our basic model (but excluding the day number and year interaction to avoid overparameterization) to the subset of our data that includes only locations that were sampled in more than one year. Seasonal profiles of daily biomass values are depicted in Supplementary Figure B6. Finally, we reran our basic model for the two (of the three) habitat clusters (for which sufficient data existed; see Biomass Data) separately in order to compare the rate of decline between them (Supplementary Figure B7).

### 3.3 Results

Following corrections for seasonal variation and habitat cluster (basic model, see Materials and Methods), the annual trend coefficient of our basic model was significantly negative (annual trend coefficient = -0.063, sd=0.002, i.e. 6.1% annual decline). Based on this result, we estimate that a major (up to 81.6% [79.7-83.4%]) decline in mid-summer aerial insect biomass has taken place since 1989 (Figure 3.2A). However, biomass loss was more prominent in mid-summer as compared to the start and end of the season (Figure 3.3A), indicating that the highest losses occur when biomass is highest during the season (Figure 3.2B). As such, a seasonally weighted estimate (covering the period 1-April to 30-October; see methods) results in an overall 76.7% [74.8-78.5%] decline over a 27 year period. The pattern of decline is very similar across locations that were sampled more than once (Figure 3.4), suggesting that the estimated temporal decline based on the entire dataset is not confounded by the sampling procedure. Re-estimation of the annual decline based on 26 locations that have been sampled in more than one year (Supplementary Figure B6), revealed a similar rate of decline (76.2%[73.9-78.3%]).

Insect biomass was positively related to temperature and negatively to precipitation (Supplementary Table B1). Including lagged effects of weather revealed no effect of either number of frost days, or winter precipitation, on the biomass in the next season (Supplementary Table B1). The overall model fit improved as compared to our basic model ( $R^2=65.4\%$ , Table 3.3), explaining within and between year variation in insect biomass, but not the overall decline ( $\log(\lambda) = -0.058$ , sd= 0.002). Over the course of the study period, some temporal changes occurred in the means of the weather variables (Supplementary Figure B4), most notably an increase by 0.5 °C in mean temperature and a decline 0.2 m/sec in mean wind speed. Yet, these changes either do not have an effect on insect biomass (e.g. wind speed) either are expected to positively affected insect biomass (e.g. increased temperature). Furthermore, a phenological shift with peak biomass earlier in the

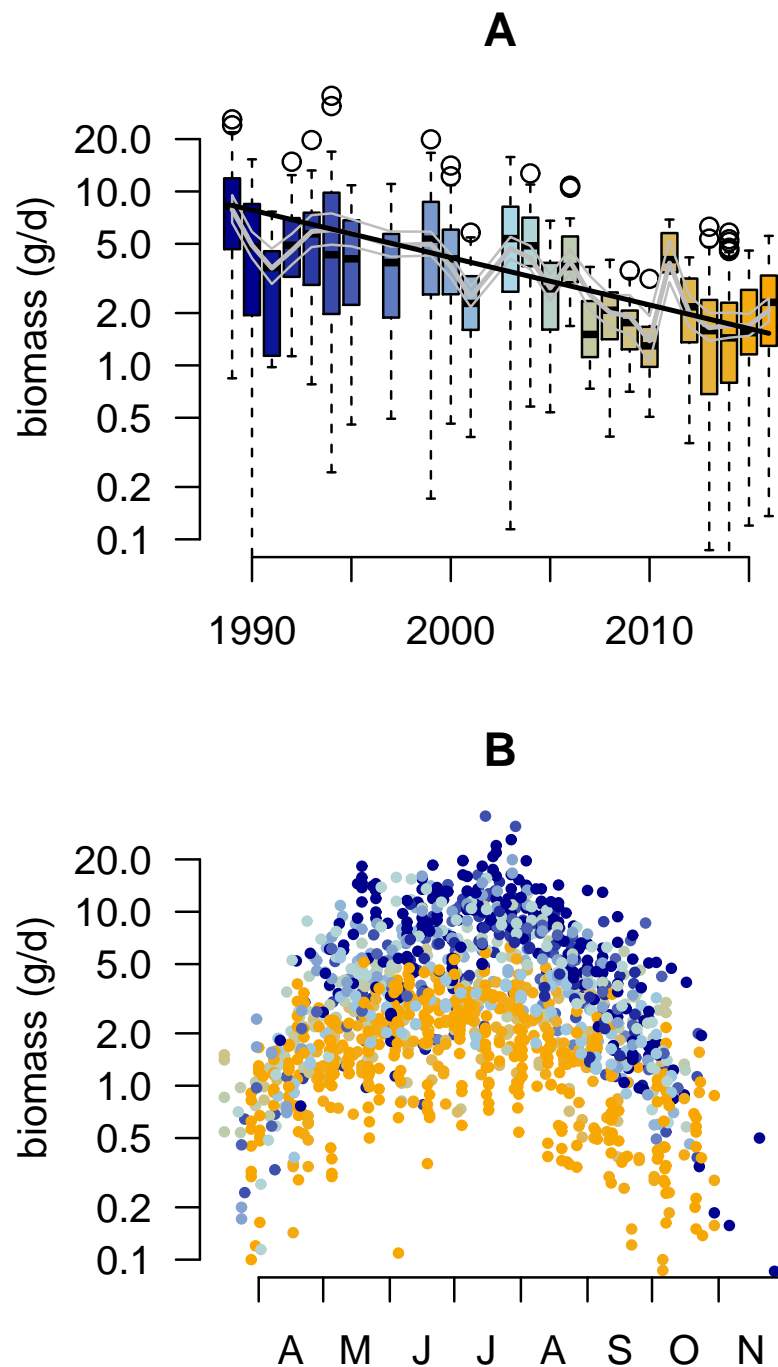


Figure 3.2: **Temporal distribution of insect biomass.** (A) Boxplots depict the distribution of insect biomass (gram per day) pooled over all traps and catches in each year ( $n=1503$ ). Based on our final model, the grey line depicts the fitted mean (+95% posterior credible intervals) taking into account weather, landscape and habitat effects. The black line depicts the mean estimated trend as estimated with our basic model. (B) Seasonal distribution of insect biomass showing that highest insect biomass catches in mid summer show most severe declines. Color gradient in both panels range from 1989 (blue) to 2016 (orange).

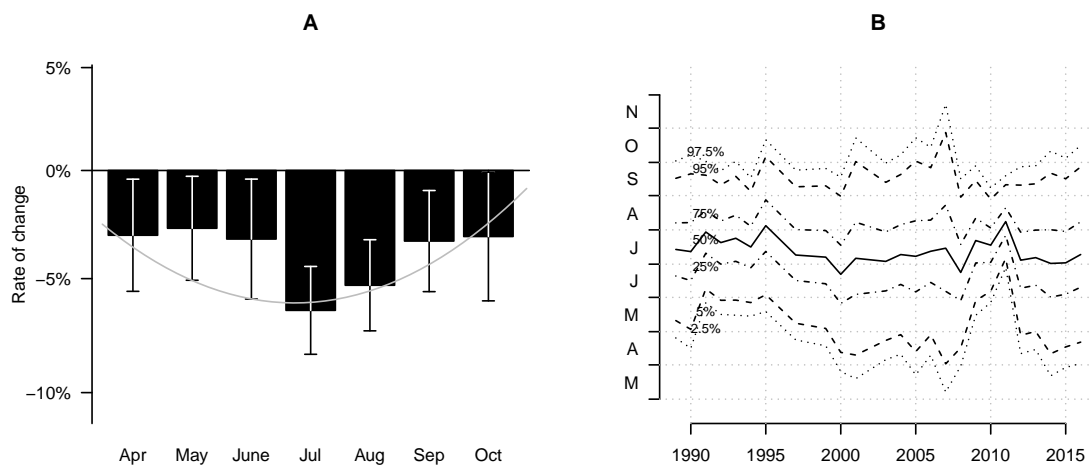


Figure 3.3: **Seasonal decline and phenology.** (A) Seasonal decline of mean daily insect biomass as estimated by independent month specific log-linear regressions (black bars), and our basic mixed effects model with interaction between annual rate of change and a quadratic trend for day number in season. (B), Seasonal phenology of insect biomass (seasonal quantiles of biomass at 5% intervals) across all locations revealing substantial annual variation in peak biomass (solid line) but no direction trend, suggesting no phenological changes have occurred with respect to temporal distribution of insect biomass.

season could have resulted in lower biomass in the mid-season (Figure 3.3A), but this does not appear to be the case as none of the seasonal distribution quantiles in biomass showed any temporal trend (Figure 3.3B).

Table 3.3: **Results for 7 models ranked by Deviance Information Criterion (DIC).** For each model, the number of parameters, the Deviance Information Criterion, the effective number of parameters (pD), calculated  $R^2$  and difference in DIC units between each model and the model with lowest  $\Delta$ DIC. See Table 3.2 for covariates included in each model.

|  | model                  | npar | Deviance | DIC      | pD    | $R^2$ | $\Delta$ DIC |
|--|------------------------|------|----------|----------|-------|-------|--------------|
|  | 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      |

There was substantial variation in trapped insect biomass between habitat clusters (see Materials and Methods), with nutrient-rich grasslands, margins and wasteland containing 43% more insect biomass than nutrient-poor heathland, sandy grassland, and dunes. Yet, the annual rate of decline was similar, suggesting that the decline is not specific to certain habitat types (Supplementary Figure B7). To further characterize trap locations, we used past (1989-1994) and present (2012-2015) aerial photographs and quantified land use

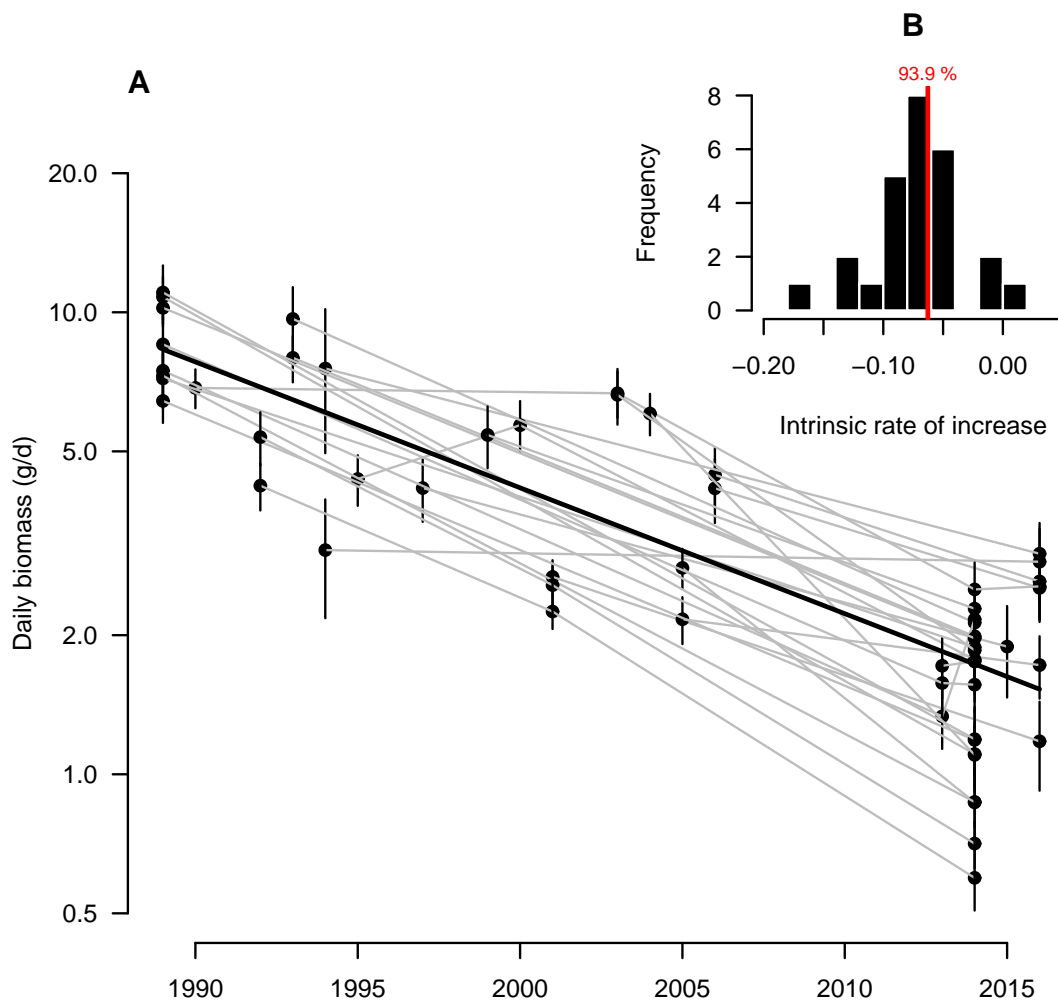


Figure 3.4: **Temporal distribution of insect biomass at selected locations.** (A) Daily biomass (mean  $\pm 1$  se) across 26 locations sampled in multiple years (see Supplementary Figure B6 for seasonal distributions). (B) Distribution of mean annual rate of decline as estimated based on plot specific log-linear models (annual trend coefficient =  $-0.053$ ,  $sd=0.002$ , i.e. 5.2% annual decline).

cover within 200m around the trap locations. On average, cover of arable land decreased, coverage of forests increased, while grassland and surface water did not change much in extent over the last three decades (Supplementary Figure B5). Overall, adding land use variables alone did not lead to a substantial improvement of the model fit ( $R^2=61.3\%$ , Table 3.3), nor did it affect the annual trend coefficient ( $\log(\lambda)=-0.064$ ,  $sd=0.002$ ). While presence of surface water appeared to significantly lower insect biomass, none of the other variables were significantly related to biomass. However, including interactions between the annual trend coefficient and land use variables increased the model fit slightly (Table 3.3), and revealed significant interactions for all variables except coverage of surface water (Supplementary Table B2). These interactions, which were retained in our final

Table 3.4: **Posterior parameter estimates of the final mixed effects model of daily insect biomass.** For each included variable, the corresponding coefficient mean, standard deviation and 95% credible intervals are given. P-values were calculated empirically based on posterior distributions of coefficients.

| Class              | Variable                              | mean   | sd    | 2.50%  | 97.50% | P     |     |
|--------------------|---------------------------------------|--------|-------|--------|--------|-------|-----|
|                    | Intercept                             | 2.450  | 0.233 | 1.983  | 2.891  | 0.000 | *** |
| Temporal           | $\log(\lambda)$                       | -0.080 | 0.007 | -0.094 | -0.067 | 0.000 | *** |
|                    | Day number                            | -0.100 | 0.028 | -0.155 | -0.045 | 0.001 | *** |
|                    | Day number <sup>2</sup>               | -0.447 | 0.029 | -0.504 | -0.392 | 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  | 0.078 | .   |
|                    | Arable land                           | -1.063 | 0.184 | -1.420 | -0.709 | 0.000 | *** |
|                    | Forest                                | -0.522 | 0.216 | -0.947 | -0.121 | 0.007 | **  |
|                    | Grassland                             | 0.819  | 0.233 | 0.367  | 1.265  | 0.000 | *** |
|                    | Water                                 | -0.327 | 0.170 | -0.659 | 0.005  | 0.027 | *   |
| Habitat            | Herb species                          | -0.054 | 0.045 | -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 | 0.010 | **  |
| Intercations       | Year $\times$ Day number              | -0.003 | 0.001 | -0.006 | -0.000 | 0.017 | *   |
|                    | Year $\times$ Day number <sup>2</sup> | 0.010  | 0.001 | 0.007  | 0.013  | 0.000 | *** |
|                    | Year $\times$ Arable land             | 0.047  | 0.008 | 0.031  | 0.064  | 0.000 | *** |
|                    | Year $\times$ Forest                  | 0.035  | 0.010 | 0.016  | 0.055  | 0.000 | *** |
|                    | Year $\times$ Grassland               | -0.059 | 0.014 | -0.086 | -0.033 | 0.000 | *** |
| Random effects     | $\sigma_{site}$                       | 0.334  | 0.037 | 0.270  | 0.412  |       |     |
| Residual variation | $\nu$                                 | 0.870  | 0.009 | 0.852  | 0.889  |       |     |

model (Table 3.4), revealed higher rates of decline where coverage of grassland was higher, while lower declines where forest and arable land coverage was higher.

We hypothesized that successional changes in plant community (Brown, 1985) or changes in environmental conditions (Nilsson *et al.*, 2008; Fox *et al.*, 2014), could have affected the local insect biomass, and hence explain the decline. Plant species inventories that were carried out in the immediate vicinity of the traps and in the same season of trapping, revealed that species richness of trees, shrubs and herbs declined significantly over the course of the study period (Supplementary Figure B5). Including species richness in our basic model, i.e. number of tree species and log number of herb species, revealed significant positive and negative effects respectively on insect biomass, but did not affect the annual trend coefficient (Supplementary Table B3), explaining some variation between locations rather than the annual trend coefficient. Moreover, and contrary to expectation, trends in herb species richness were weakly negatively correlated with trends in insect biomass, when compared on per plot basis for plots sampled more than once. Ellenberg values of plant species provide a reliable indicator for the environmental conditions such as pH, nitrogen, and moisture (Ellenberg, 1974; Ellenberg *et al.*, 1992). Around trap locations, mean indicators (across all locations) were stable over time, with changes in the order of less than 2% over the course of the study period. Adding these variables to our basic

model revealed a significant positive effect of nitrogen and light, and a significant negative effect of Ellenberg temperature on insect biomass, explaining a major part of the variation between the habitat types. However, Ellenberg values did not affect the insect biomass trend coefficient ( $\log(\lambda) = -0.059$ ,  $sd = 0.003$ , Supplementary Table B3) and only marginally improved the model fit ( $R^2 = 61.9\%$ , Table 3.3). All habitat variables were considered in our final model (Table 3.4), with the exception of pH and moisture.

Our final model, based on including all significant variables from previous models, revealed a higher trend coefficient as compared to our basic model ( $\log(\lambda) = -0.081$ ,  $sd = 0.006$ , Table 3.4), suggesting that temporal developments in the considered explanatory variables counteracted biomass decline to some degree, leading to an even more negative coefficient for the annual trend. The marginal net effect of changes in each covariate over time (see Analysis), showed a positive contribution to biomass growth rate of temporal developments in arable land, herb species richness, and Ellenberg Nitrogen, while negative effects of developments of tree species richness and forest coverage (Figure 3.5). For example, the negative effect of arable land on biomass (Table 3.4), in combination with a decrease in coverage of arable land (Supplementary Figure B5), have resulted in a net positive effect for biomass (Figure 3.5). Projections of our final model, while fixing the coefficient for the temporal annual trend  $\log(\lambda)$  to zero, suggest insect biomass would have remained stable, or even increased by approximately 8% (mean rate = 1.075, 0.849-1.381) over the course of the study period.

### 3.4 Discussion

Our results document a dramatic decline in average airborne insect biomass of 76% (up to 82% in midsummer) in just 27 years for protected nature areas in Germany. This considerably exceeds the estimated decline of 58% in global abundance of wild vertebrates over a 42-year period to 2012 (WWF International, 2016; Ceballos *et al.*, 2017). Our results demonstrate that recently reported declines in several taxa such as butterflies (Thomas *et al.*, 2004; Kuussaari *et al.*, 2007; van Swaay *et al.*, 2013; Habel *et al.*, 2016; Thomas, 2016), wild bees (Goulson *et al.*, 2008; Nilsson *et al.*, 2008; Winfree *et al.*, 2009; Potts *et al.*, 2010; Ilyinykh, 2011; Ollerton *et al.*, 2014; Woodcock *et al.*, 2016) and moths (Conrad *et al.*, 2002, 2006; Fox, 2013; Fox *et al.*, 2014), are in parallel with a severe loss of total aerial insect biomass, suggesting that it is not only the vulnerable species, but the flying insect community as a whole, that has been decimated over the last few decades. The estimated decline is considerably more severe than the only comparable long term study on flying insect biomass elsewhere (Shortall *et al.*, 2009). In that study, 12.2m high suction traps were deployed at four locations in the UK over the time period 1973-2002, and showed a biomass decline at one of the four sites only. However, the sampling designs differ considerably between the two studies. Suction traps mainly target high-flying insects, and in that study the catches were largely comprised of flies belonging to the Bibionidae family. Contrary, malaise traps as used in the present study target insects flying close to the ground surface (up to 1 meter), with a much wider diversity of taxa. Future investigations should look into how biomass is distributed 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), the number of repetitions (i.e. multiple years of seasonal distributions at the same

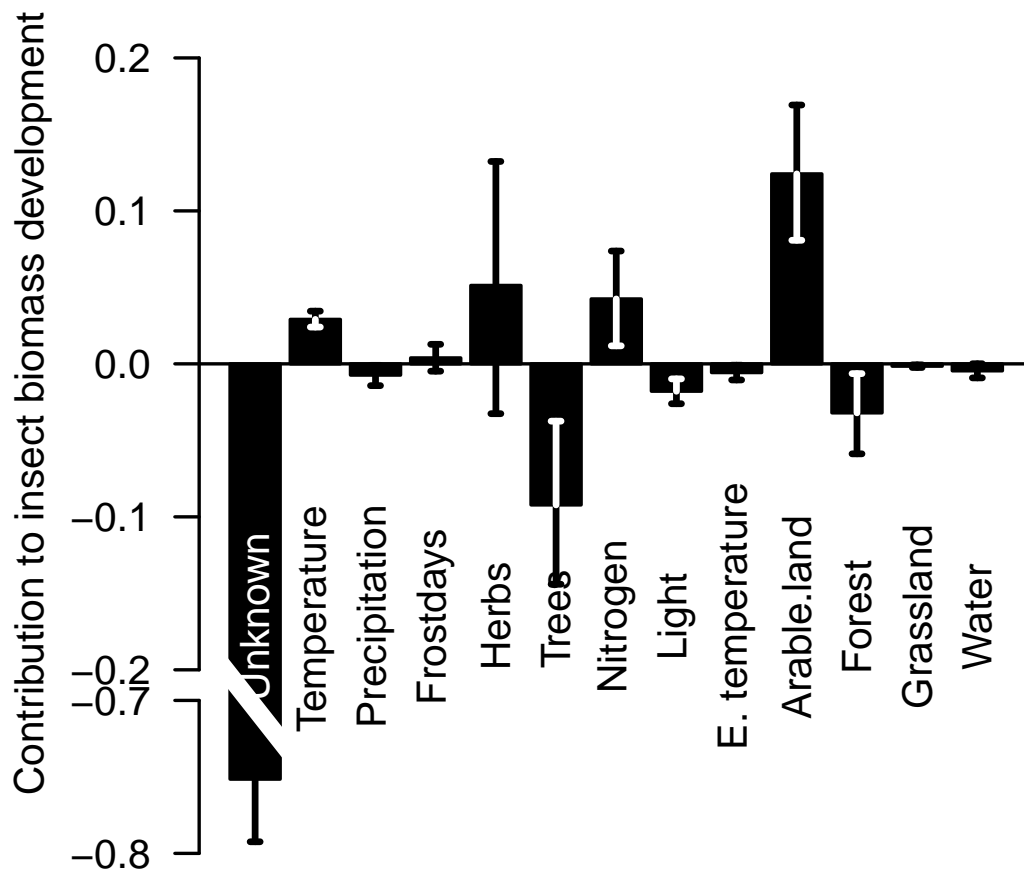


Figure 3.5: **Marginal effects of temporal changes in considered covariates on insect biomass.** Each bar represents the rate of change in total insect biomass, as the combined effect of the relevant coefficient (Table 3.4) and the temporal development of each covariate independently (Supplementary Figures B4 and B5).

locations) was lower ( $n=26$ ). We are however confident that our estimated rate of decline in total biomass resembles the true rate of decline, and is not an artifact of site selection. Firstly, our basic model (including an annual rate of decline) outperformed the null-model (without an annual rate of decline;  $\Delta\text{DIC}=822.62$  units; Table 3.3), while at the same time, between-plot variation (i.s.  $\sigma_{site}$ ) and residual variation ( $v$ ) decreased by 44.3 and 9.7% respectively, after incorporating an annual rate of decline into the models. Secondly, using only data from sites at which malaise traps were operating in at least two years, we estimated a rate of decline similar to using the full dataset (Figure 3.4), with the pattern of decline being congruent across locations (Supplementary Figure B6). Taken together, there does not seem to be evidence that spatial variation (between sites) in this dataset forms a confounding factor to the estimated temporal trend, and conclude that our estimated



biomass decline is representative for lowland protected areas in west Germany.

In light of previously suggested driving mechanisms, our analysis renders two of the prime suspects, i.e. landscape (Benton *et al.*, 2002; Nilsson *et al.*, 2008; Fox *et al.*, 2014) and climate change (Conrad *et al.*, 2002; Fliszkiewicz *et al.*, 2012; Fox *et al.*, 2014; Morecroft *et al.*, 2002), as unlikely explanatory factors for this major decline in aerial insect biomass in the investigated protected areas. Habitat change was evaluated in terms of changes in plant species composition surrounding the standardized trap locations, and in plant species characteristics (Ellenberg values). Land use changes was evaluated in terms of proportional surface changes in aerial photographs, and not for example changes in management regimes. Given the major decline in insect biomass of about 80%, much stronger relationships would have been expected if changes in habitat and land use were the driving forces, even with the somewhat crude parameters that were at our disposal.

The decline in insect biomass, being evident throughout the growing season, and irrespective of habitat type or landscape configuration, suggests large-scale factors must be involved. While some temporal changes in climatic variables in our study area have taken place, these either were not of influence (e.g. wind speed), or changed in a manner that should have increased insect biomass (e.g. temperature). However, we have not exhaustively analysed the full range of climatic variables that could potentially impact insect biomass. For example prolonged droughts, or lack of sunshine especially in low temperatures might have had an effect on insect biomass (Dennis & Sparks, 2007; Grüebler *et al.*, 2008; Ewald *et al.*, 2015; McDermott Long *et al.*, 2017). Agricultural intensification (Benton *et al.*, 2002; Fox, 2013) (e.g. pesticide usage, year-round tillage, increased use of fertilizers and frequency of agronomic measures) that we could not incorporate in our analyses, may form a plausible cause. The reserves in which the traps were placed are of limited size in this typical fragmented West-European landscape, and almost all locations (94%) are enclosed by agricultural fields. Part of the explanation could therefore be that the protected areas (serving as insect sources) are affected and drained by the agricultural fields in the broader surroundings (serving as sinks or even as ecological traps) (Battin, 2004; Öckinger & Smith, 2007; Gilroy & Sutherland, 2007; Furrer & Pasinelli, 2016). Increased agricultural intensification may have aggravated this reduction in insect abundance in the protected areas over the last few decades. Whatever the causal factors responsible for the decline, they have a far more 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 in protected areas that are meant to preserve ecosystem functions and biodiversity. While the gradual decline of rare insect species has been known for quite some time (e.g. specialized butterflies (Warren *et al.*, 2001; Nilsson *et al.*, 2008)), our results illustrate an ongoing and rapid decline in total amount of airborne insects active in space and time. Agricultural intensification, including the disappearance of field margins and new crop protection methods has been associated with an overall decline of biodiversity in plants, insects, birds and other species in the current landscape (Benton *et al.*, 2002; Thomas *et al.*, 2004; Hallmann *et al.*, 2014). The major and hitherto unrecognized loss of insect biomass that we report here for protected areas, adds a new dimension to this discussion, because it must have cascading effects across trophic levels and numerous other ecosystem effects. There is an urgent need to uncover the causes of this decline, its geographical extent, and to understand the ramifications of the decline for ecosystems and ecosystem services.

## Acknowledgments

CH and EJ were supported by the Netherlands Organization for Scientific Research (NWO grants 840.11.001 and 841.11.007), and NH by the Triodos Foundation. The investigations of the Entomological Society Krefeld and its members are spread over numerous individual projects at different locations and in different years. Grants and permits that have made this work possible are listed below:

Bezirksregierungen Düsseldorf & Köln, BfN - Bundesamt für Naturschutz, Land Nordrhein-Westfalen - Europäische Gemeinschaft ELER, Landesamt für Agrarordnung Nordrhein-Westfalen, Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen, Landesamt für Umwelt Brandenburg, Landesamt für Umwelt Rheinland-Pfalz, LVR - Landschaftsverband Rheinland, Naturschutzbund Deutschland, Nordrhein-Westfalen Stiftung, RBN – Bergischer Naturschutzverein, RVR - Regionalverband Ruhr, SGD Nord Rheinland-Pfalz, Universitäten Bonn, Duisburg-Essen & Köln, Untere Landschaftsbehörden: Kreis Düren, Kreis Heinsberg, Kreis Kleve, Kreis Viersen, Kreis Wesel & AGLW, Stadt Düsseldorf, Stadt Köln, Stadt Krefeld, Rheinisch Bergischer Kreis, Rhein Kreis Neuss & Rhein-Sieg-Kreis. Members of the Entomological Society Krefeld and cooperating botanists and entomologists that were involved in the empirical investigations are greatly acknowledged: U.W. Abts, F. Bahr, A. Bäumler, D. & H. Beutler, P. Birnbrich, U. Bosch, J. Buchner, F. Cassese, K. Cölln, A.W. Ebmer, R. Eckelboom, B. Franzen, M. Grigo, J. Günneberg, J. Gusenleitner, K. Hamacher, F. Hartfeld, M. Hellenthal, J. Hembach, A. Hemmersbach, W. Hock, V. Huisman-Fiegen, J. Illmer, E. Jansen, U. Jäckel, F. Koch, M. Kreuels, P. Leideritz, I. Loksa, F. B. Ludescher, F. J. Mehring, G. Milbert, N. Mohr, P. Randazzo, K. Reissmann, S. Risch, B. Robert, J. de Rond, U. Sandmann, S. Scharf, P. Scherz, J. Schiffer, C. Schmidt, O. & W. Schmitz, B. P. & W. Schnell, J. L. Schönfeld, E. Schraetz, M. Schwarz, R. Seliger, H. W. Siebeneicher, F. & H. Sonnenburg W. J. S. & P. Sorg, A. Ssymank, H. Sticht, M. Weithmann, W. Wichard and H. Wolf.





## 4. Declining abundance of beetles, moths and caddisflies in the Netherlands

Collection of insects. Photo credit: EvK Krefeld

Hallmann, C. A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van Deijk, J., van Steenis, W., Jongejans, E. (2019). Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity*. doi: 10.1111/icad.12377.

### 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 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 1985-2016. However, 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.

## 4.1 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-Gutiérrez *et al.*, 2016) and moths (Groenendijk & Ellis, 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 datasets 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 datasets (each from a single location or area, using different approaches) covering a wide range of insect families, to provide further insights in 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 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 datasets, 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.*, 2019a). 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

- To assess the trends in abundance of various insects at the species and order level,
- To assess the trend in biomass of macro-moths and ground beetles, and
- To assess how species-trends vary along species-specific trait axes.

## 4.2 Materials and methods

Data were collected at two groups of sites: De Kaaistoep and Wijster. For each site we describe the sampling protocols, dataset and statistical analysis. A summary description of available data is given in 4.1. 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.

Table 4.1: **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. Separate species trends are performed on a subset of species for which enough data were available (numbers indicated between brackets).

| Order                                 | Location  | Sites | Years                                     | Samples     | Individuals | Species  |
|---------------------------------------|-----------|-------|---|-------------|-------------|----------|
| <i>Lepidoptera</i>                    | Kaaistoep | 1     | 21: 1997:2017                             | 497 nights  | 54492       | 477(178) |
| <i>Coleoptera</i>                     | Kaaistoep | 1     | 21: 1997:2017                             | 572 nights  | 257793      | 123(76)  |
| <i>Trichoptera</i>                    | Kaaistoep | 1     | 10: 2006,2009:2017                        | 261 nights  | 33540       |          |
| <i>Ephemeroptera</i>                  | Kaaistoep | 1     | 10: 2006,2009:2017                        | 255 nights  | 9713        |          |
| <i>Neuroptera</i>                     | Kaaistoep | 1     | 10: 2006,2009:2017                        | 258 nights  | 936         |          |
| <i>Hemiptera</i>                      | Kaaistoep | 1     | 10: 2006,2009:2017                        | 258 nights  | 49747       |          |
| <i>Coleoptera</i><br><i>Carabidae</i> | Wijster   | 48    | 26: 1986:1997,<br>2002:2003,<br>2005:2016 | 26 years    | 264986      | 156(98)  |
| <i>Coleoptera</i><br><i>Carabidae</i> | Wijster   | 31    | 16: 2002:2017                             | 15672 weeks | 99075       |          |

### 4.2.1 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 Felix & van Wielink (2008). Insects were attracted by light in combination with a white cloth (Supplementary Figure C1) over a period of 3.3 hours per trapping night, normally starting around sunset (Figure 4.1c). During that period individuals of insect taxa were counted, or 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 van Wielink & 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 1997-2017 period 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 48000 of 239000 beetle specimens.

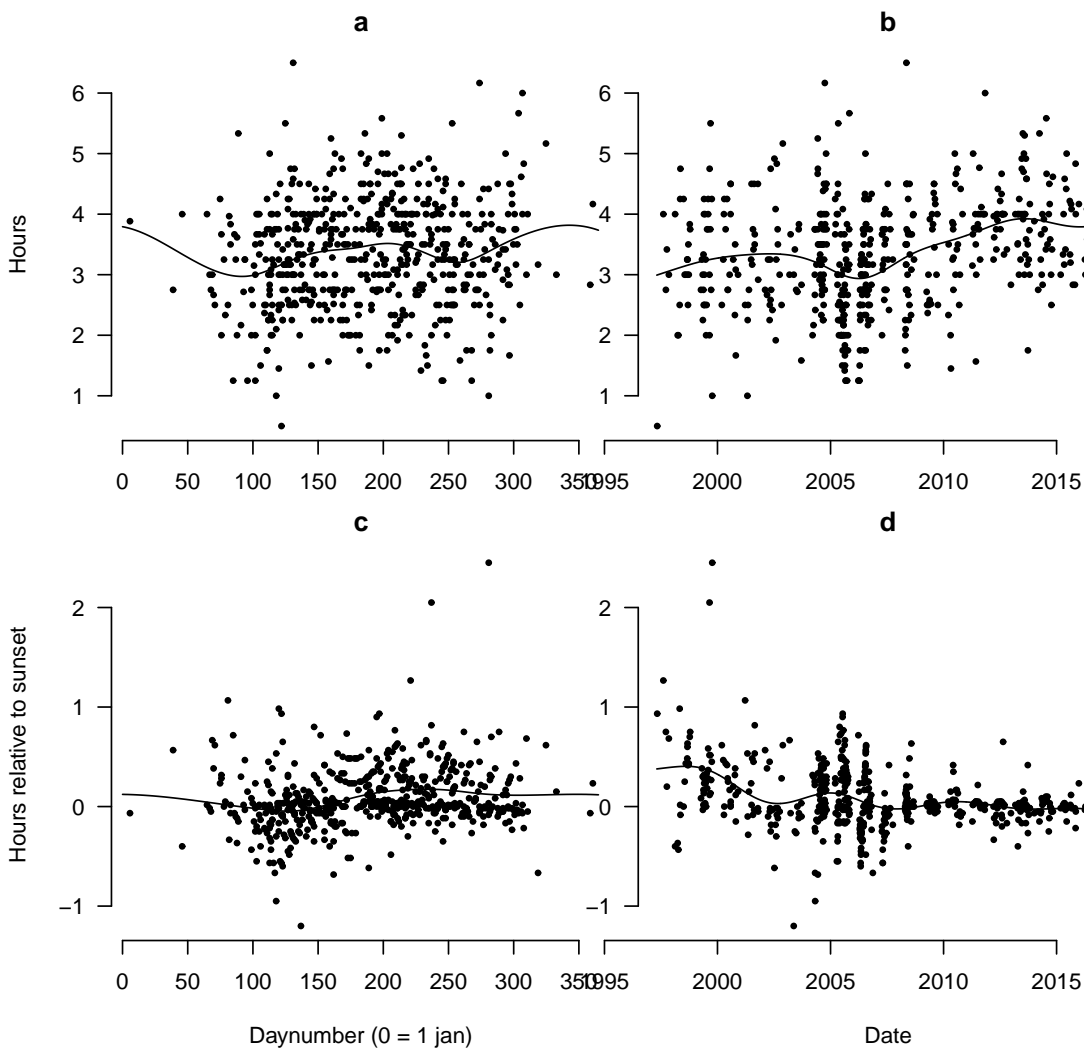


Figure 4.1: **Sampling characteristics for De Kaaistoep dataset.** **a:** Number of sampling hours per evening plotted against day of the year (1 = 1 January). **b:** Number of sampling hours per evening per year. **c:** Start of sampling relative to sunset (in hours) versus day of the year. **d:** Start of sampling relative to sunset per year.

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 (Figure 4.1a), but did increase from an average of 3.1 hours (1997-2009) to an average of 3.8 hours per night after 2010 ( $F=48.98$ ,  $d.f.=572$ ,  $p<0.001$ ; Figure 4.1b). 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 (Figure 4.1c&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 ( $F=1.568$ ,  $emphp=0.211$ ). To analyse trends for each order (or species)  $k$ , we modeled the counts in year  $t$  and on day  $d$  using Generalized Additive Models (GAM Wood, 2006) and assuming a negative-binomial distribution (White & Bennetts, 1996) and a log link to the predictors. GAMs were deemed more appropriate than Generalized 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 (Supplementary Table C1). 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 ( $\gamma_s(d)$ ) 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 standardized 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.

#### 4.2.2 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 1990's. 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 ( $25\times 25\text{cm}$ ) were installed (Supplementary Figure C2): one lethal funnel trap with a 3% formaldehyde solution, and 2 live traps. The traps at each location were spaced 10 meters apart. Caught ground beetles (Coleoptera: Carabidae) have been identified at weekly intervals. Further details on the sampling protocol and the area are given in den den Boer & 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 1986-2016 (Table 1), and secondly, the weekly sums per species and location that have been fully digitized and checked: 2002-2017.

Annual totals 1986-2016. In total, 7,778 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 Generalized Additive Models 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 (Supplementary Table C2). 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-May), and separately over the summer months (June-August). Additionally, we also included quadratic effects of each variable. Each weather covariate in  $W$  (including the squared values) was standardized 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 one year and 10 locations only sampled in two 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 two and ten 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 modeling 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 6 different model formulations (Supplementary Table C3). Location was included in all models as a random effect.

### 4.2.3 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. However, 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 dataset 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:

$$mass_k = 0.032 \times length_k^{2.63} \quad (4.1)$$

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 Supplementary Material 5), we analyzed those summary data in a log-log regression analysis with sample size as the weight of the records. Superfamily-specific residuals ( $\epsilon_k$ ) 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:

$$mass_k = \exp(-5.144 + 3.018 \times \log(length_k) + \epsilon_k) \quad (4.2)$$

where for instance the effect sizes ( $\epsilon_k$ ) 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 dataset) or day  $d$  (for macro-moths in De Kaaistoep dataset):

$$B_t = \sum_{k=1}^K B_{k,t} \quad (4.3)$$

and where  $B_{k,t} = Y_{k,t} \times mass_k$ , 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  $M_4$  (Supplementary Table C1) and for the Wijster data model  $A_1$  (Supplementary Table C2).

#### 4.2.4 Trend classification

We classified order-specific and species-specific trends in abundance and biomass, based on estimates of the annual trends coefficient  $\rho$  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  $\rho$  associated with p-values larger than 0.05 were classified as ‘uncertain declines’. Declines were labeled ‘severe’ when significant  $\rho$  values were lower than -0.05. More information on these trend classifications can be found in Supplementary Table C4.

### 4.2.5 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 (4 classes: as egg, caterpillar, pupa or adult; Ebert, 2005; Waring & Townsend, 2015, [www.lepidoptera.se](http://www.lepidoptera.se), assessed 18 April 2019), 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 explanation above). Host plant type class “other” included several species of heath, and mosses and lichens. Using data from Habel *et al.* (2019b), 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.* (2019b), 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 specialization (four classes: from stenotopic (i.e. specialised to one or few habitats) to very eurytopic (i.e. habitat generalist)), distribution type (4 classes marginal, submarginal, sub central and central), and the log of species weight. Habitat specialization 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, 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 generalized 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:

$$V(y) = \sigma^2 \exp(2 \times \phi \times \log(y)) \quad (4.4)$$

where  $\phi$  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.

## 4.3 Results

### 4.3.1 Collecting at light at De Kaaistoep

Across insect orders, models including weather variables always prevailed over models without weather variables (Supplementary Table C5). 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 hours in the period 1997-2006 to an average of 3.8 hours in 2009-2017 (Figure 4.1b), fitted trends over the study period were slightly lower when correcting for sampling duration (Supplementary Figure C3). Hence, we derived annual trends while accounting for weather variables and sampling duration (See Supplementary Table C6 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 Figure 4.2. 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 summarized in Table 4.2. 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 ( $\rho = 0.010$ ,  $se = 0.058$ ,  $p\text{-value}=0.87$ ), and we therefore labeled 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 ( $\rho=-0.070$ ,  $se=0.033$ ,  $p\text{-value}=0.033$ ).

**Table 4.2: 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. See Supplementary Table C4 for the scheme of the significance evaluation of the trends. See the main text for a discussion about the uncertainty concerning the Ephemeroptera trend.

| Insect order  | Annual trend coefficient ( $\rho$ ) | % 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              |

Trends of macro-moth species were variable, with on average a decline of 4% per year (Figure 4.3a). 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 (Figure 4.3b). Declines of individual species were positively, but not significantly, related to mean abundance (mean number of individuals per trapping night;  $t\text{-value}=0.861$ ,  $p\text{-value}=0.392$ ).

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 4.3). The species-rich family of ground beetles (Carabidae) dominated these results, with numeric declines (totals within family) of ground beetles declining steeper

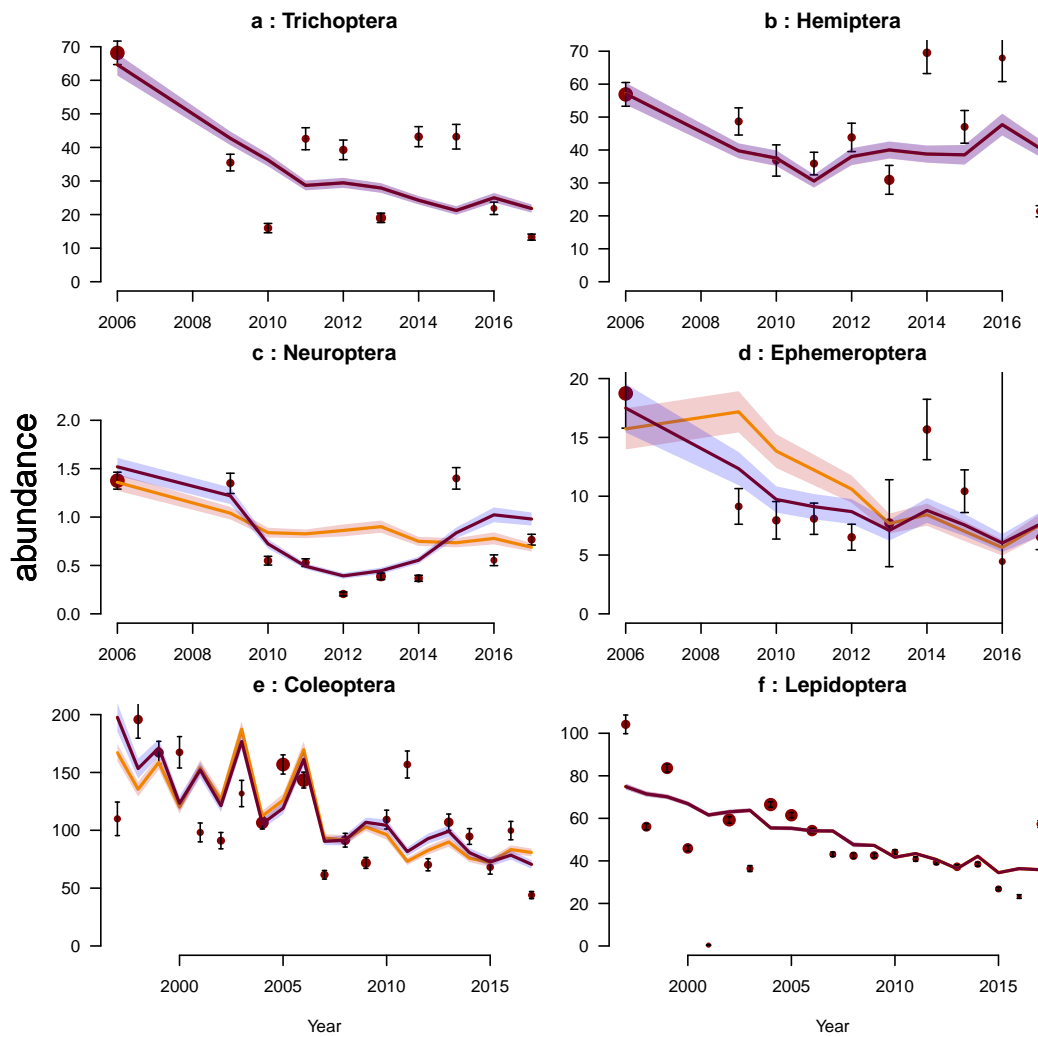


Figure 4.2: Trends in numbers counted per evening of six orders of insects at De Kaaistoep. For each order, the annual indices (points, model  $M_3$ ), and estimates of the linear (orange, model  $M_4$ ) and nonlinear (blue, model  $M_5$ ) trends are given. Evidence for non-linearity is only apparent in Neuroptera, Ephemeroptera and Coleoptera, while for the remainder of the orders models  $M_4$  and  $M_5$  are indistinguishable.

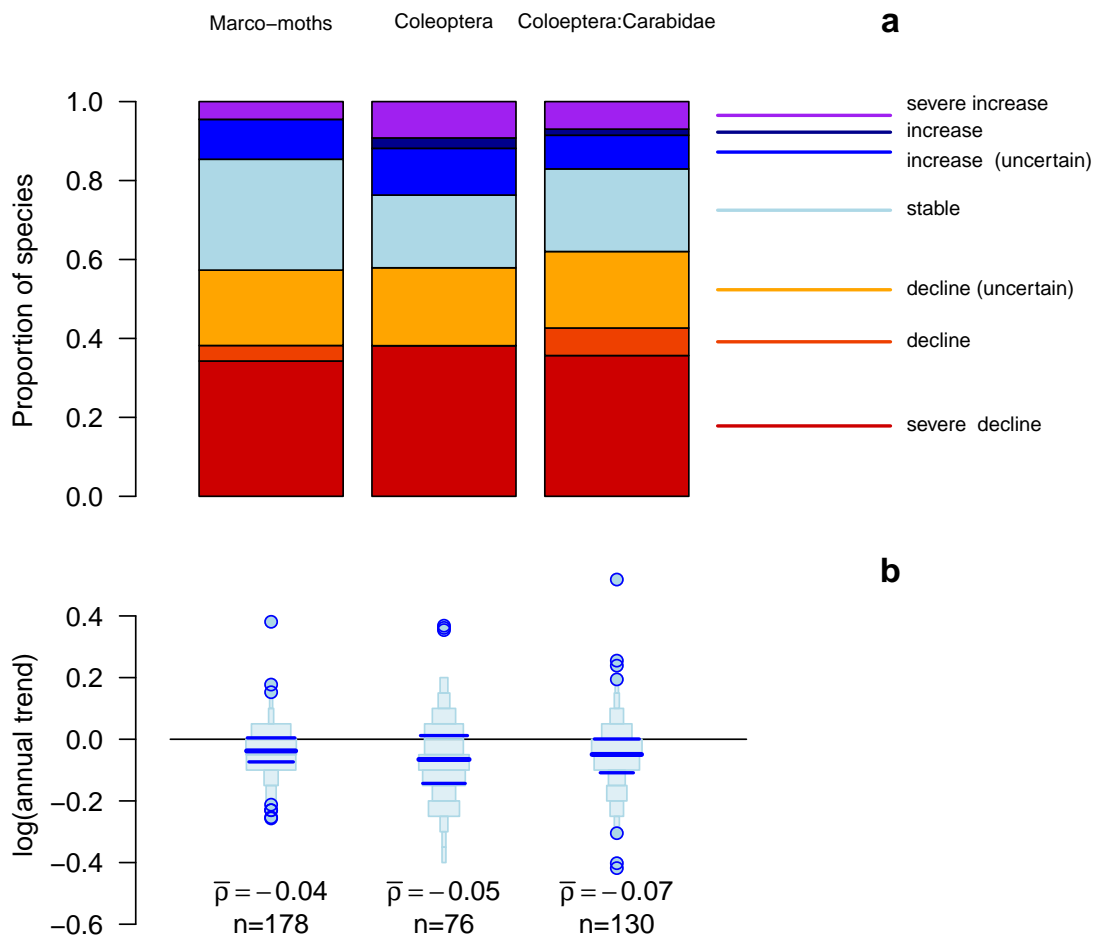


Figure 4.3: **Log of annual trend coefficient** ( $\rho$ ) of species of macro-moths ( $n=178$ ) and beetles in De Kaaistoep ( $n=76$ ) as well as ground beetles in Wijster ( $n=130$ ). **a**: Barplots depicting trend classifications. **b**: Distribution of trend coefficients.

( $\rho=-0.090$ ,  $se=0.021$ ,  $p\text{-value}<0.001$ ) than those of ladybirds (Coccinellidae, excluding the invasive exotic *Harmonia axyridis*,  $\rho=-0.029$ ,  $se=0.012$ ,  $p\text{-value}=0.001$ ), whereas carrion beetles (Silphidae,  $n=4$ ) were found to significantly increase ( $\rho=0.035$ ,  $se=0.016$ ,  $p\text{-value}=0.003$ ). 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 (Supplementary Figure C4).

### 4.3.2 Pitfall traps near Wijster

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. However, non-linear trends explained year totals significantly better than linear models ( $AIC_{nl}=3768.26$ ,  $d.f.=35.54$  versus  $AIC_l=3773.63$ ,  $d.f.=33.48$ ). Models considering weather variables did not improve model fit, regardless of whether they were measured over spring (March-May) or summer (June-August). Hence, we present trends based on models that omit weather effects. The linear trend coefficient was significantly negative ( $\rho=-0.044$ ,  $se=0.006$ ,  $p\text{-value}<0.001$ , 4% decline per year, Figure 4). Results of the non-linear trend model however showed that the trend initially increased, followed by a decline starting after 1995 (Figure 4.5). The linear annual trend since 1995 showed even steeper declines ( $\rho=-0.060$ ,  $se=0.009$ ,  $p\text{-value}<0.001$ ), 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 two 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 4 sampling years made the trend even more negative (5.5% annual rate of decline, Supplementary Figure C5).

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 (Figure 4.3a), 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 (Figure 4.3b).

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 (Supplementary Table C7). However, 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% ( $\rho=-0.077$ ,  $se=0.002$ ,  $p\text{-value}<0.001$ ) for the period 2002-2017 (Supplementary Figure V6).

### 4.3.3 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 ( $\rho=-0.036$ ,  $se=0.006$ ,  $p\text{-value}<0.001$ , i.e. -3.3%,  $se=0.52$  mg/year; Figure 4.5a). For the ground beetles near Wijster, we estimated the average decline in total biomass to be 2% ( $se=0.48$ ) annually (Fig. 4.5b), which is considerably less than that of numbers per species or total sums of individuals. However, considering only

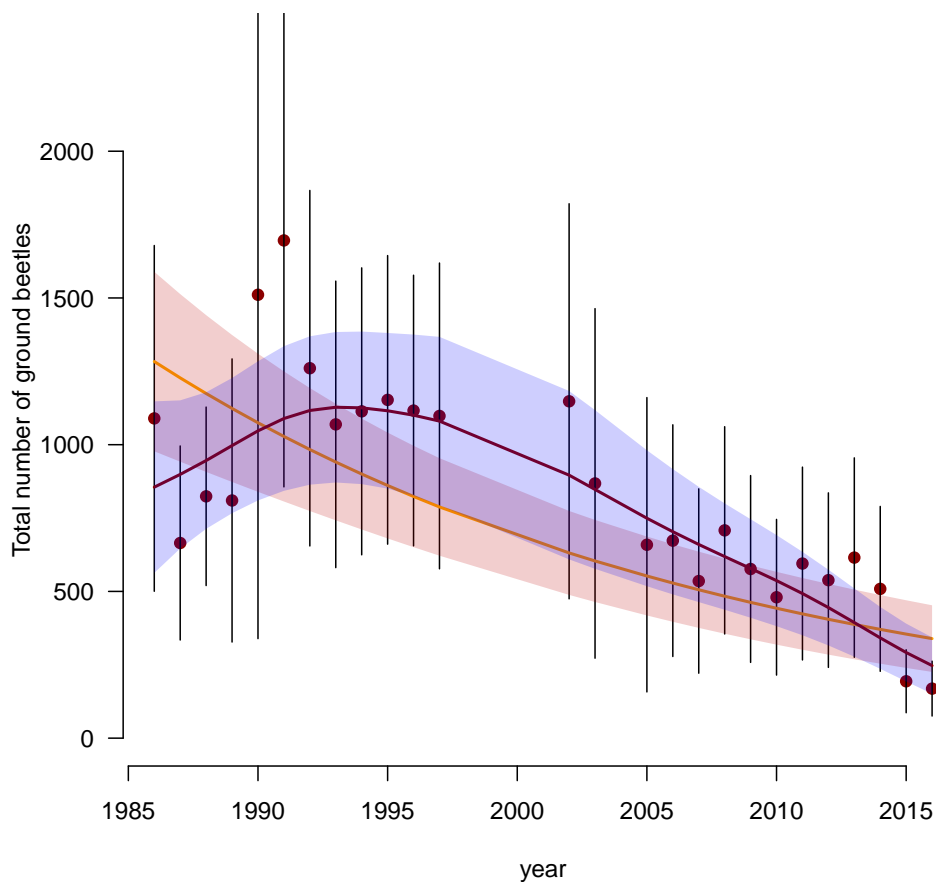


Figure 4.4: **Trends in total numbers of ground beetles** (Coleoptera: Carabidae) in pitfalls near Wijster

the period after 1995, the rate of decline in biomass appeared a lot more severe ( $\rho=-0.0414$ ,  $se=0.006$ ,  $p\text{-value}<0.001$ ), implying an on average 4.1% ( $se=0.53$ ) decline per year.

#### 4.3.4 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,  $p < .0001$ , for macro-moths, and 25.99,  $p < .0001$ , 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 (Supplementary Table C8), with species depending on grass, herbs or diverse host plant species declining most (Figure 4.6, Supplementary Table C9). 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; Supplementary Table C10). For ground beetles in the Wijster area, lower intrinsic rates were observed among species that are considered



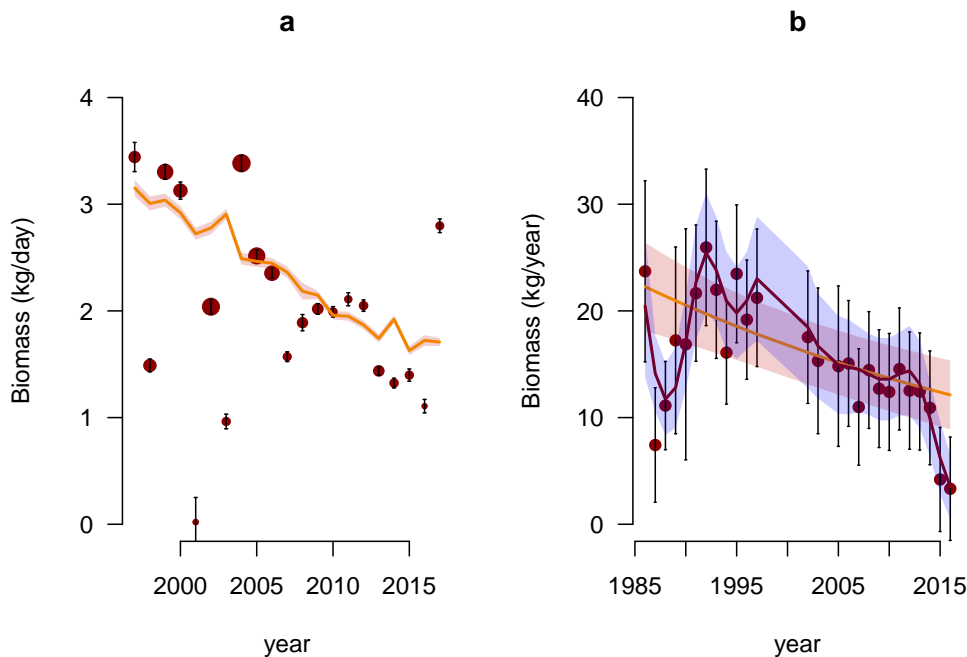


Figure 4.5: **Biomass trend of (a) macro-moths (Lepidoptera) per trapping night at De Kaaistoep and (b) ground beetles (Coleoptera: Carabidae) per year from pitfalls near Wijster.** For each order, the annual indices (points), and estimates of the linear (orange) and nonlinear (blue,) trends are given. 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.

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 (Figure 4.7, Supplementary Tables C11 and C12).

## 4.4 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 out 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; Homburg et al., 2019; Schuch et al., 2019), concerns with

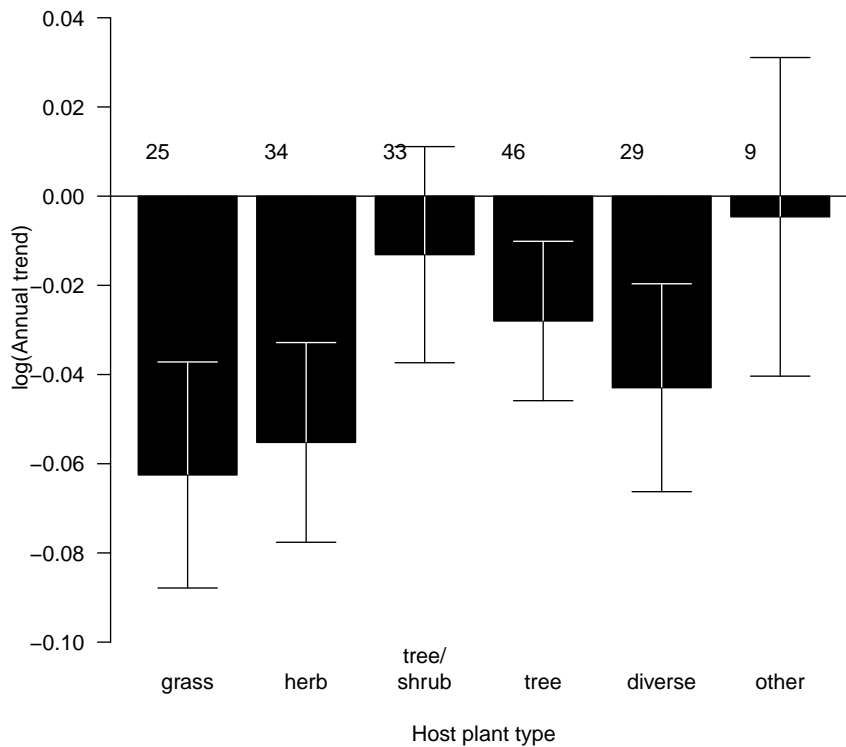


Figure 4.6: **Mean log annual trend coefficient** ( $\rho$ , +95% confidence levels) of macro-moth species (in De Kaaistoep) with various types of host plants. The number of macro-moth species are indicated for each host plant category.

respect to 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. However, since only two areas are included in this analysis, it is hard to generalize 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 (-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, were less negative than the average of the individual species trend (totals -6%, mean species trend -7%, biomass -4%). Additionally, following corrections of

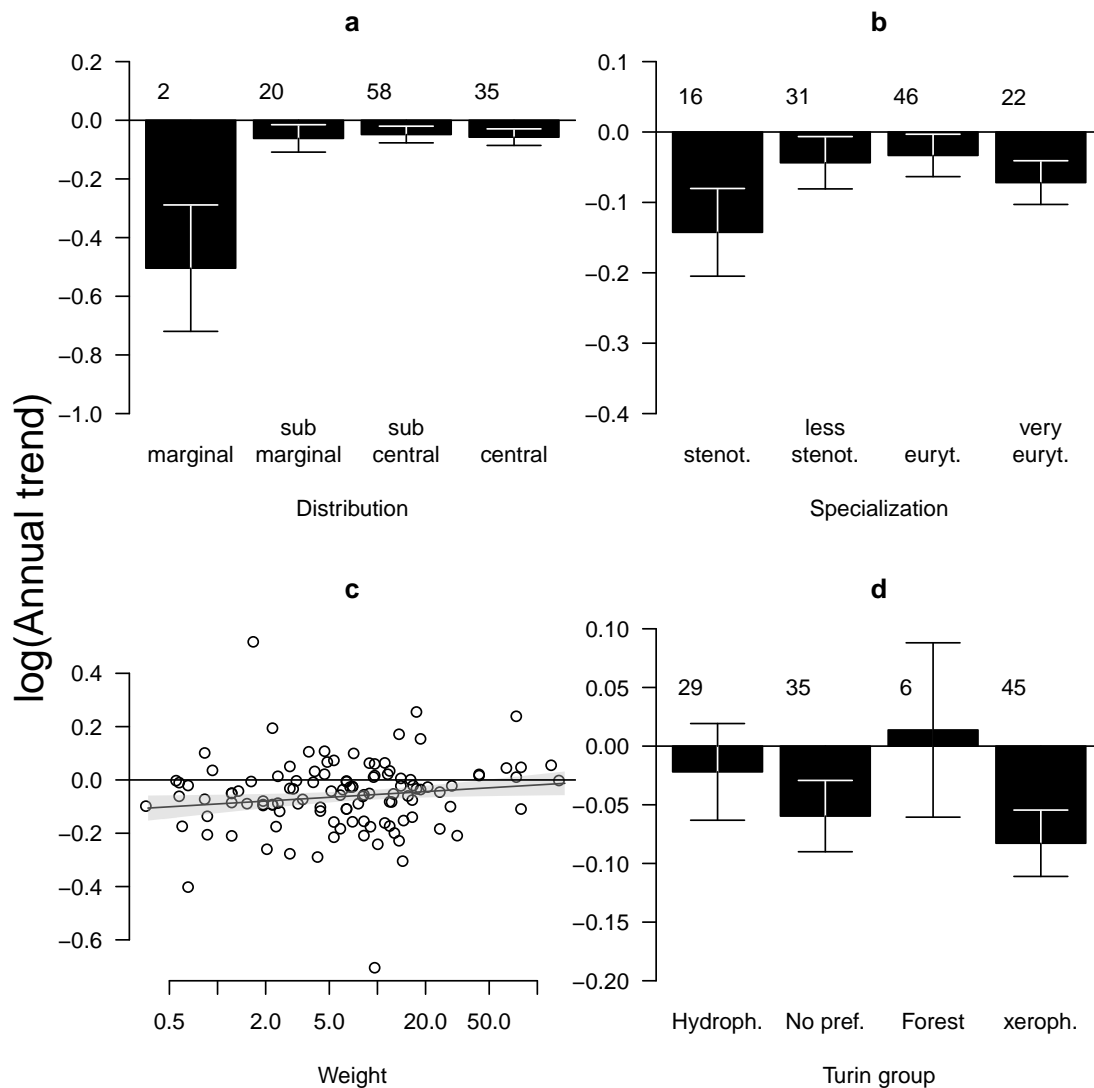


Figure 4.7: **Mean log annual trend coefficient** ( $\rho$ , +95% confidence levels) of ground beetle species (in the Wijster region) for different levels of (a) distribution (ranging from species in the Netherlands being in the margin of their distribution to more in the center), (b) specialization (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)).

several traits, a positive effect was found of weight on species trend (Fig. 7c). Here, the less 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 starts 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 specialized 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 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 of carrion-beetles (Silphidae) can be explained by carrion experiments done at approximately 25 meters from the light source in 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 (for example larvae of Odonata) showed positive population trends in a stream in De Kaaistoep about 1 kilometer from the collection site (van Wielink & Spijkers, 2012). However, for dragonflies, Termaat *et al.* (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. 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, pesticide leaching) or natural (e.g. succession) factors.

In both datasets, 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 has 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 behavior 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 dataset 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. However, 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, Supplementary Figure C5). 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.

## 4.5 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).

Standardized 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.

## Acknowledgements

We are grateful for the permission to perform insect monitoring on land owned by TWM Gronden BV and Natuurmonumenten. We are grateful for Natuurmonumenten, the Uyttenboogaart-Eliassen Foundation and the Netherlands Organisation for Scientific Research (NWO-grant 841.11.007) for financial support. We are also grateful to Piet den Boer, who started the Wijster data collecting in 1959 already and Alje Woltering for field assistance in the Wijster region. Guido Stoker assisted in the macro-moth monitoring at De Kaaistoep in 2016 and 2017. Ron Felix identified part of the Carabidae of De Kaaistoep. Willem Ellis entered data (1995-2015) in the Noctua database. Hans Turin helped with the trait database for ground beetles. All authors declare no conflict of interest.



A close-up photograph of a male hoverfly (Myathropa florea) perched on a white flower (Heracleum). The hoverfly has a yellow and black striped abdomen and transparent wings. The background is a soft-focus green and white.

## 5. Biomass declines predict diversity loss in a hoverfly community

A male specimen of *Myathropa florea*, on *Heracleum*. Photo credit: Martin Sorg

Hallmann, C. A., Ssymank, A., Sorg, M., Jongejans, E., de Kroon, H. Biomass declines predict diversity loss in a hoverfly community. *In prep.*

### Abstract

Reports from lowland Germany have emphasized a dramatic decline in the biomass of flying insects. However, to what extent and how the biomass decline reflects biodiversity loss is still an open question. Here, we analyze a novel dataset on the abundance of hoverflies (*Diptera: Syrphidae*) as collected with six malaise traps in 1989 and 2014. Our analysis of nearly 20000 individuals of 162 species, reveals that total flying biomass reflects abundance and richness of hoverflies remarkably well. The decline in biomass is paralleled by a loss of 20% in species richness and 80% in total abundance over a period of 25 years. However, the daily availability of species declined by 75%, and in general a decline in both diversity and evenness was observed, particularly in spring and early summer. Persistence rates of species were lower for intermediate and common species than expected given their relative abundance in 1989.



## 5.1 Introduction

Recent reports from lowland Germany have emphasized a dramatic decline in the biomass of flying insects in protected areas. In less than 30 years, the biomass of flying insects has decreased by more than 75% (Hallmann *et al.*, 2017), a finding that questions both the stability of ecosystems in contemporary land use, as well the sustainability of ecosystem services. An important unknown aspect, is to what extent the reported insect biomass decline represents diversity loss, including functional diversity. A 75% drop in insect biomass over less than three decades can hardly be envisaged without cascading trophic effects (Nebel *et al.*, 2010; Hallmann *et al.*, 2014; English *et al.*, 2018), or without disruption in pollination (Biesmeijer *et al.*, 2006; Potts *et al.*, 2010) and nutrient cycling (Speight, 1989) as a consequence. Yet, much of these potentially far-reaching consequences will depend on the nature of decline with respect to the abundance, diversity, and ecological role, of the species in question. Hence, there is an urgent need to unravel whether and how the biomass decline translates into biodiversity declines.

Although the decline of total flying biomass is likely to reflect a decline in the abundance of flying insects, decline rates may be distributed disproportionately among the species that make up the flying insect community. Specialist and less mobile species in well monitored insects such as wild bees, butterflies and moths, were usually first to disappear from communities (Biesmeijer *et al.*, 2006; Potts *et al.*, 2010; Ollerton *et al.*, 2014), while more recently there have been indications that common and widespread species are in decline as well, particularly, species of intermediate abundance, or less mobile species (Conrad *et al.*, 2006; Van Dyck *et al.*, 2009; Habel & Schmitt, 2018). Further more, the decline in biomass may not be equally distributed among species of different size. For example, Scheper *et al.* (2014) found larger wild bees to decline at a faster rate in the Netherlands over the past century as compared to smaller species. A similar study in Canada showed increased declining proportions of largest invertebrate prey in the diet of an insectivorous birds (English *et al.*, 2018). Hence, a decline in biomass of flying insects may reflect species loss, a decline in abundance, a decline in the weight distribution of the species, or any combination of these processes. The consequences for pollination, food supply and other ecological functions may depend critically on which of these aspects is predominant.

Here we set out to answer a number of prevailing questions with respect to the observed biomass decline. We examine how daily biomass samples relate to the decline of a group well represented by malaise traps, the hoverflies (Syrphidae). Hoverflies as a family are considered an important wild pollinator (Larson *et al.*, 2001; Ssymank *et al.*, 2008, 2009), an important agent in biocontrol (Chambers & Adams, 1986; Colley & Luna, 2000; Rojo *et al.*, 2003), suitable as bioindicator (Sommaggio, 1999), and hence a potentially informative group of insects, representative for a variety of ecological functions. All hoverfly individuals caught in six locations in two seasons that were 25 years apart (1989 vs. 2014) were identified at the species level, amounting up to nearly 20,000 individuals of 162 species from in a total of 59 genera. Our objectives were threefold. We investigated how samples of total flying insect biomass reflect declines in diversity components of hoverflies during and over the season. Secondly, we compared the rate of decline in seasonal total abundance and species richness between these two years. Thirdly, we examined how decline rates and persistence probabilities among species are related to species abundance. We discuss our results in light of a number of potential causal factors

that may have been responsible for the decline of hoverflies and other taxa.

## 5.2 Methods

### 5.2.1 Data

We utilize data obtained from six malaise traps in the Wahnbachtal, (Northrhine-Westphalia, Germany, 50°51'7"N, 7°19'15"E), that were deployed in 1989 and again in 2014. Traps were situated in wet meadows as well as tall perennial meadows, in close proximity to shrub corridors, forest-grassland borders and to the Wahnbach river, and surrounded by agricultural land, essentially a rather heterogeneous habitat. The Wahnbach river and the greater part of the valley are protected for watershed purposes, and are subject to nature conservation management by the Wahnbach Talperrenverband. Hence, several restrictions apply to safeguard against water contamination.

Total insect biomass collected with these traps were already included in Hallmann *et al.* (2017), but here we focus on new information: the abundance and richness of hoverflies (*Syrphidae*) in each of the collected samples. Methodology of collection are described in Sorg (1990); Schwan *et al.* (1993); Sorg *et al.* (2013); Hallmann *et al.* (2017) and Szymank *et al.* (2018). In brief, malaise traps were deployed throughout the vegetative period, and operated continuously (day and night). Malaise trap construction (e.g. size, material, colouring and ground sealing) and placing (e.g. positioning, orientation and slope of the locations) were standardized in all aspects. Insect samples were preserved at 80% ethanol solution. Catches of the six traps investigated in the present study were emptied regularly: on average exposure intervals were 7.0 days (sd = 0.5) in 1989 and 16.7 days (sd=5.6) in 2014. Across the six traps in 2014 the total exposure time (in number of days) was 42% higher as compared to 1989. All collected pots (n=196) were used in the present analysis with in total 19604 individual hoverflies counted, distributed over 162 species and 59 genera. In Table 5.1 we further provide summary statistics relevant for sample size descriptions.

In order to assess how environmental conditions have changed over the 25 years, several additional datasets were assembled. Vegetation inventories along with expert assessment of management practices, were performed each time a trap was deployed at a given location (See Supplementary Table D3). Aerial photographs allowed to investigate broad changes in the landscape surrounding the trap locations. Virtually no landscape changes were observed in this area in terms, and hence we did not include landscape variables in our analysis. Furthermore, climatic data were obtained from 169 climatic stations, and were used to interpolate daily weather variables to each trap location, using spatio-temporal kriging. These steps are described in Hallmann *et al.* (2017). Seasonal profiles of temperature, precipitation and wind speed are given in Supplementary Figure D1.

### 5.2.2 Analysis overview

Our analysis consists of three components. First, we considered total abundance, species richness, and species diversity, at two temporal scales: pooled in each year, i.e. across the sampling season (see section 5.2.3), and seasonally (i.e. per day, see section 5.2.4), and compared these metrics between 1989 and 2014. Secondly, we examined how total flying biomass (i.e. the weight of all trapped insects, of which hoverflies are only a small

proportion) related to total abundance as well as species richness of hoverflies (section 5.2.5). Thirdly, we derived persistence probabilities and population growth rate trends per species, in order to examine interspecific variation in these parameters (see section 5.2.6).

### 5.2.3 Pooled species richness and diversity

We pooled data across traps in each year, and compared species richness and diversity between the two sampling years. Because of unequal sampling length between the two years (see Table 5.1), we calculated the change in species richness between 1989 and 2014 using two methods. First, we used the chao (Chao, 1987; Chiu *et al.*, 2014) estimator for species richness, as it has been found to perform best among competing estimators (Palmer, 1990).

$$\hat{S}_{chao} = S + \hat{f}_0 = S + \frac{n-1}{n} f_1 \frac{f_1 \times 0.5}{f_2} \quad (5.1)$$

- where  $S$  the observed richness,  $n$  the samples size, and  $f_k$  the number of species with exactly  $k$  detections, i.e.  $f_1$  the number of singletons,  $f_2$  the number of doubletons, while  $f_0$  the (unobserved) number of species not detected. Secondly, changes in species richness between the two sampling years were also assessed by means of species accumulation curves against exposure time.

To compare diversity between the two years, we computed the Shannon's diversity index ( $H'$  Shannon, 1948)

$$H' = - \sum (n_j / \sum(n_j) \times \log(n_j / \sum(n_j))) \quad (5.2)$$

- as well as Pielou's evenness index ( $e$ ) for each year

$$e = H' / \log(S_{chao}) \quad (5.3)$$

where  $S_{chao}$  the expected number of species, as defined above.

To better visualize how dominance and diversity changed between the two years, we fitted rank abundance curves (Whittaker, 1965) to the hoverfly data. We initially considered five common distributions (*broken-stick*, *pre-emption*, *log-normal*, *zipf* and *zipf-mandelbrod* Wilson, 1991; Oksanen *et al.*, 2018) but for both datasets the zipf-mandelbrod distributions had a superior fit. We therefore only report results on the fitting of this rank distribution. The zipf-mandelbrod rank-abundance distribution is given by

$$\hat{n}_r = N \times \frac{e^{\beta_0 * \log(r + \beta_1)}}{\sum(e^{\beta_0 * \log(r + \beta_1)})} \quad (5.4)$$

where  $\beta_0$  and  $\beta_1$  parameters shape the decline in abundance with increasing species rank.

### 5.2.4 Daily activity-abundance, species richness and diversity

We considered the total abundance (number of hoverflies), number of species, and diversity (Shannon diversity and evenness indices) at a finer temporal scale, in addition to the analysis integrating data across the sampling years. At this finer temporal scale of analysis, sampling and environmental effects are likely to be more pronounced in the response variables as compared to the pooled analysis. For example, abundance is measured through

the number of individuals trapped, which in turn depends on both trap (and sample) exposure length (longer intervals trap more insects) as well as the environmental conditions (e.g. weather) affecting the activity of species during the exposure period of a sample. Furthermore, contrary to abundance, species richness does not act additively with respect to exposure period length, i.e. we do not expect a monotonic increase in richness with sampling interval length, but rather a nonlinear increase approaching an asymptote akin to the species-area relationship.

To allow comparison of abundance and species richness between the two years, we developed a model that accounts for environmental and sampling processes, by modeling the daily values of the response variable using a latent variable approach (Hallmann *et al.*, 2017), and where sample expectations are aggregated over daily expectations of the corresponding exposure interval. Parameter estimates were obtained by fitting three parallel MCMC chains using the JAGS samplers (Plummer *et al.*, 2003) and R (R Core Team, 2015b) using 12000 iteration, a burnin period of 2000 samples and a thinning interval of 10 samples to account for serial chain autocorrelation. Inference was thus based on 3000 posterior samples for each parameter.

**Total daily abundance.** Let  $N_j$  be the total number of individuals observed in each pot  $j$ , collected between day  $\tau_{1,j}$  and  $\tau_{2,j}$ , and let  $Y_j$  be its expectation under a Poisson process:

$$N_j \sim \text{Poisson}(Y_j) \quad (5.5)$$

In turn, the expectation per pot is the sum of the (unobserved) daily expectations over the corresponding exposure interval:

$$Y_j = \sum_{t=\tau_1}^{\tau_2} y_{j,t} \quad (5.6)$$

where  $y_{j,t}$  is the latent number of individuals on a given day  $t$  in pot  $j$ , which in turn is modeled as a function of a number of covariates (see Parameterization).

**Observed and expected daily species richness.** Let  $q_{j,t} = y_{j,t}/Y_j$  be the proportion of the total abundance on day  $t$  of the exposure interval of pot  $j$ . Also let  $N_{i,j}$  be the observed abundance of species  $i$  in pot  $j$ . Under the assumption that  $q_{j,t}$  is invariant with respect to species, the expected abundance of each species in each day is given as the latent multinomial sample  $n_{i,j,t} \sim \text{Multinomial}(q_{j,t}, N_{i,j})$ .

The number of species expected to have been trapped on day  $t$  is then simply

$$S_{t,j} = \sum_{i=1}^K X_{i,j,t} \quad (5.7)$$

- where  $X_{i,j,t} = 1$  if  $n_{i,j,t} > 0$ , and 0 otherwise. Next, to account for imperfect detection (not all species present on a particular day are likely to have been trapped), we relied on the Chao's estimator to derive the number of species expected to be present:  $\hat{s}_{t,j}$ . To this end, we tracked doubletons ( $f_2$ ) and singletons ( $f_1$ ) for each exposure day in the MCMC samples, and computed the expected richness using equation 5.1. Finally, based on the posterior samples we computed indices of diversity and evenness (equations 5.2 and 5.3) to describe seasonal diversity components and community structure.

**Parametrization** The daily expectations of total number of hoverfly individuals were modeled as a function of year ( $yr$ ), a seasonal components (day number  $\tau$ , where 0 = January 1), weather effects (temperature, wind speed and precipitation) and an effect for each trap (five contrasts)

$$\log(y_{i,\tau}) = \alpha_N + \beta_{N,year} \times X + f_N(\tau) + f_N(climate) + \beta_{N,trap} \quad (5.8)$$

where  $f(\tau) = \beta_\tau^{(1)} \times \tau + \beta_\tau^{(2)} \times \tau^2$  and  $f(climate) = \sum_{i=1}^3 (\beta_{clim}^i \times C_i)$ , with  $C_i$  representing each weather variable  $i$ . Prior to analysis, weather and seasonal covariates were scaled to unit variance and zero mean.

Using the posterior estimates of expected daily richness ( $S_{t,j}$ ), we also derived the rate of decline in richness between the two years, while at the same time accounting for weather and sampling effects. To accomplish this, we used expected richness estimates  $\hat{s}_{t,j}$  as response in a Poisson error structure (allowing for overdispersion), and a log link:

$$\log(\hat{s}_{t,trap}) = \alpha_s + \beta_{s,year} \times X + f_s(\tau) + f_s(climate) + \beta_{s,trap} \quad (5.9)$$

This was performed for each of the MCMC iterations, and results were summarized over the posterior distributions of the coefficients.

### 5.2.5 Relationship to biomass

We compared within-year profiles of total flying-insect biomass between Wahnbachtal and all other sites analyzed in Hallmann *et al.* (2017) in the periods 1989-1992 and 2013-2015 ( $n=15$  and  $29$  respectively), which allowed us to infer how representative the six malaise traps included in this study compared to the regional biomass distribution and trend (see Supplementary Figure D3).

In order to infer how total flying insect biomass related to the abundance of hoverflies, we regressed the log of the number of individuals per pot against the log of the biomass per pot. We used simple linear regression with Gaussian error and with separate slope and intercept for each year, and examined whether simpler models (e.g common slope across years) were more parsimonious.

$$N_j = \psi + \phi B_j \quad (5.10)$$

where  $\psi$  and  $\phi$  are the intercept and slope coefficients relating abundance to biomass ( $B_j$ ).

We did not expect a linear relationship between biomass and hoverfly richness, but rather a curvilinear one, mediated by the species~abundance relationship. In order to relate the number of species to total flying insect biomass of a given pot, we used rarefaction theory (Hurlbert, 1971). The number of species expected to be trapped in pot  $j$ , depends on the number of individuals trapped ( $N_j$ ) total richness ( $S$ ) and relative abundance of each species ( $N_i$ ). Additionally, it depends on the seasonal activity of each species, as not all species may be available to be trapped during each exposure period of each pot. The expected number of species in pot  $j$  given total pot abundance  $N_j$  is given by

$$\hat{s}_j(N_j, S) = c \times \sum_i^S \left( 1 - \frac{\binom{N-N_i}{N_j}}{\binom{N}{N_j}} \right) \quad (5.11)$$

which essentially represents sampling without replacement. The summation is taken over all species observed ( $S$ , here across locations and years), and results in the rarefied richness from a total of  $N$  individuals (ever counted across locations and years) to the total abundance  $N_j$  of pot  $j$ . Parameter  $c$  represents the average specie's seasonal availability (see Appendix 6.3). To produce the relationship between richness and biomass (see figure 5.1), we replaced  $N_j$  in equation 5.11 with the mean expectation of abundance given biomass from equation 5.10.

### 5.2.6 Persistence and rates of change by species

We examined variation in the persistence probabilities between species (i.e. the probability of a species being present in 2014, given its presence in 1989). To analyse persistence, we used generalized linear models (GLM) with species presence in 2014 (conditional on presence in 1989,  $n=141$  species) as response, assuming a binary error distribution and a logit link. As persistence probabilities depend to a large extent on initial abundance, more rare species have diminished probability of persistence as a result of environmental and demographic stochasticity (Caughley, 1994). Hence we included the log-abundance of each species in 1989 as covariate.

$$\log\left(\frac{\hat{p}_i}{1-\hat{p}_i}\right) = a_p + b_p \times \log(n_{i,1989}) \quad (5.12)$$

The fitted logistic regression (based on observations) was compared to the expected persistence probability for each species, assuming a uniform per capita decline rate across species. The expected probability of persistence  $z_i$  for the  $i$ -th species given a rate of decline  $\lambda$ , is given by

$$z_i = P(X_i > 0) = 1 - (1 - \lambda)^{n_{i,1989}} \quad (5.13)$$

where we defined the rate of decline in total abundance of species present in 1989 as

$$\lambda = \frac{\sum_1^K n_{i,2014}}{\sum_1^K n_{i,1989}} \quad (5.14)$$

For species present in both years ( $n=81$ ) we modeled the abundance in 2014 using a generalized linear model with a Poisson error structure and a log link.

$$\log(n_{i,2014}) = a_n + b_n \times \log(n_{i,1989}) \quad (5.15)$$

Here too, we compared this observed species abundance to the expected abundance in 2014, assuming a uniform per capita decline rate across species. The expected abundance of each species in 2014  $n_{i,2014} = \lambda \times n_{i,1989}$  given  $n_{i,1989} > 0$ , is given as

$$b_i = \frac{\sum_{x=1}^{\infty} (x \times p(x))}{z_i} \quad (5.16)$$

for all  $x \geq 1$ , and where

$$p(x) = \binom{n_{i,2014}}{x} \lambda^x (1 - \lambda)^{[n_{i,2014} - x]} \quad (5.17)$$

## 5.3 Results

### 5.3.1 Raw hoverfly data

The raw (uncorrected) total number of species, total number of individuals, and total insect biomass were found to have decreased by 44.2, 84.5, and 76.1% from 1989 to 2014 (25 years), despite the longer exposure period of the Malaise traps in 2014. Out of the in total 162 species, 81 were seen in both years, 60 were seen only 1989 and 21 only in 2014. The average densities (numbers trapped per day) of species caught in both years ( $n=81$ ) amounted to 0.218 ( $se=0.046$ ,  $N=15279$ ) individuals per species and per day in 1989 and 0.026 ( $se=0.009$ ,  $N=2584$ ) individuals per species per day in 2014. The average densities of species present only in 1989 were 0.033 ( $se=0.011$ ,  $N=1687$ ), while the average densities of species seen only in 2014 were 0.002 individuals ( $se=0.001$ ,  $N=54$ ) per day.

Table 5.1: **Summary of hoverfly data.** For each trap and year the number of pots, total exposure time (in days), the total number of hoverfly species and individuals, and the biomass of all flying insects are given.

| Trap no. | N. pots |      | Exposure time |      | N. species |      | N. individ |      | Biomass |      |
|----------|---------|------|---------------|------|------------|------|------------|------|---------|------|
|          | 1989    | 2014 | 1989          | 2014 | 1989       | 2014 | 1989       | 2014 | 1989    | 2014 |
| 1        | 20      | 13   | 140           | 216  | 96         | 52   | 2084       | 394  | 949     | 416  |
| 2        | 20      | 12   | 140           | 182  | 86         | 28   | 3222       | 122  | 1508    | 223  |
| 3        | 21      | 13   | 146           | 216  | 73         | 56   | 2005       | 516  | 898     | 240  |
| 4        | 21      | 13   | 146           | 216  | 95         | 66   | 4091       | 417  | 1429    | 423  |
| 5        | 21      | 12   | 146           | 184  | 75         | 45   | 3504       | 953  | 1020    | 178  |
| 6        | 20      | 10   | 140           | 200  | 91         | 38   | 2060       | 236  | 1453    | 257  |
| $\Sigma$ | 123     | 73   | 864           | 1220 | 141        | 102  | 16966      | 2638 | 7257    | 1737 |

### 5.3.2 Climate and habitat

Temperature was similar between the two years, while 1989 had more precipitation than 1989, and also was somewhat windier. (Supplementary Figure D1). No consistent change in the number of species in the herb layer between the two years was observed, although great variation was observed in plant richness between years and traps (Supplementary Figure D5).

### 5.3.3 Total flying biomass and hoverfly abundance and richness

The seasonal patterns of flying insect biomass captured in 1989 and 2014 in Wahnachtal were comparable to that considering all pots in Hallmann *et al.* (2017) of the periods 1989-1992 and 2012-2015 respectively (Supplementary Figure D3), suggesting that the six traps are representative for the regional developments in terms of biomass and its decline over time.

The total number of individuals per pot, correlated linearly with total flying biomass (on the log-log scale; Figure 5.1), which suggests that biomass, as used in Hallmann *et al.* (2017) is a reliable indicator for the abundance of hoverfly species. The relationship of number individuals to total flying biomass changed from 1989 to 2014 in both intercept and slope (model with and without interaction,  $LRT:F=6.5$ ,  $p=0.012$ ,  $d.f.=87$ ,  $R^2=75.05\%$ , Figure 5.1a), suggesting that less hoverflies were trapped for each additional gram of

total insect biomass in 2014 as compared to 1989. Additionally, we did not observe any significant difference in the distribution of log-body size of the species (Supplementary Figure D7) between the two years, suggesting that the decline in biomass is not related to a shift in weight distribution, but rather driven solely by loss in abundance.

Similarly, Hoverfly species richness was non-linearly related to biomass (Figure 5.1b), with the increase in richness declining at larger biomass samples (See Supplementary Methods), as a consequence of the non-linearity of the species accumulation curve against cumulative exposure time (Figure 5.2a). Hence, these results suggest that total flying biomass is not only indicative to total abundance, but also to species richness of hoverflies.

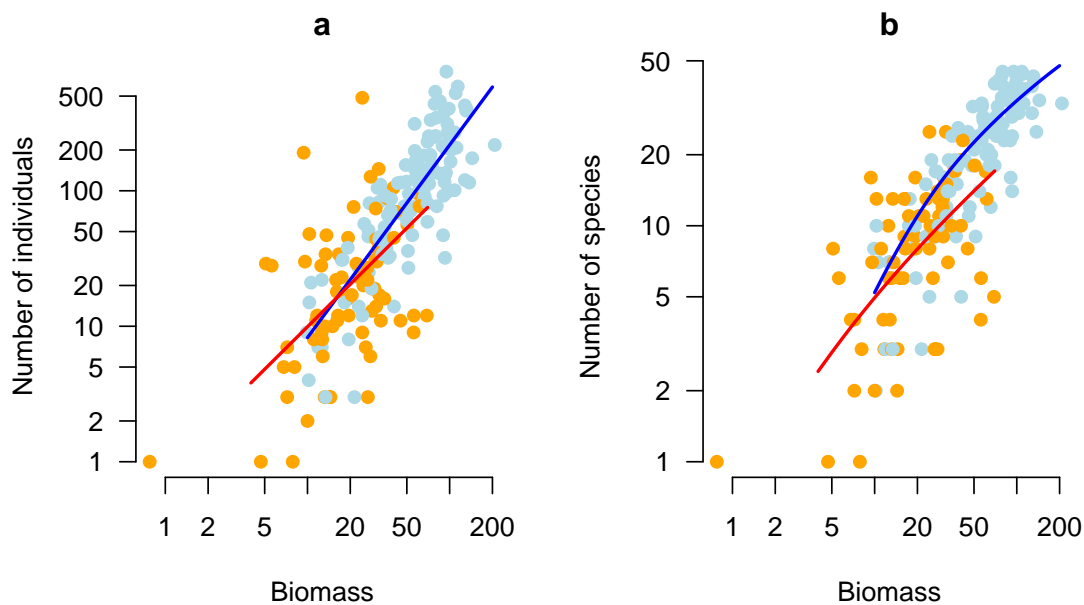


Figure 5.1: **Relationships between total biomass of flying insects and (a) total number of hoverfly individuals, and (b) number of hoverfly species.** Blue and red points depict data of 1989 and 2014 respectively, while blue and red lines depict year-specific fitted relationships.

#### 5.3.4 Pooled diversity

The accumulation curves (i.e. the number of species accumulated with cumulative exposure time, pooled over the six traps) over exposure time showed a higher asymptote in 1989 as compared to 2014 (Figure 5.2a). Non-parametric estimates of richness (for pooled data over sites and samples in each year) suggested declines in richness. Chao's estimate project a richness of 161.40 (se=10.93) species in 1989 against 125.04 (se=11.21) in 2014 (Figure 5.2a). Based on these estimates, we expect a species loss of 22.5%, against a decline of 27.7% for the uncorrected number of species trapped.

Overall, a lower diversity was observed in 2014 (Shannon index:  $H_{1989}=3.52, H_{2014}=2.92$ ), and the relative abundance of the species were less even in 2014 (Pielou index:  $e_{1989} : 0.692, e_{2014} : 0.605$ ). Between the years, rank-abundance curves showed an initial steeper drop in the abundance of the common species in 2014 than in 1989 (Figure 5.2b), indicating a higher dominance among abundant species. However, the slope of log abundance to



species rank appeared very comparable between the two years for species at the tenth or higher rank positions (see Supplementary Figure D2).

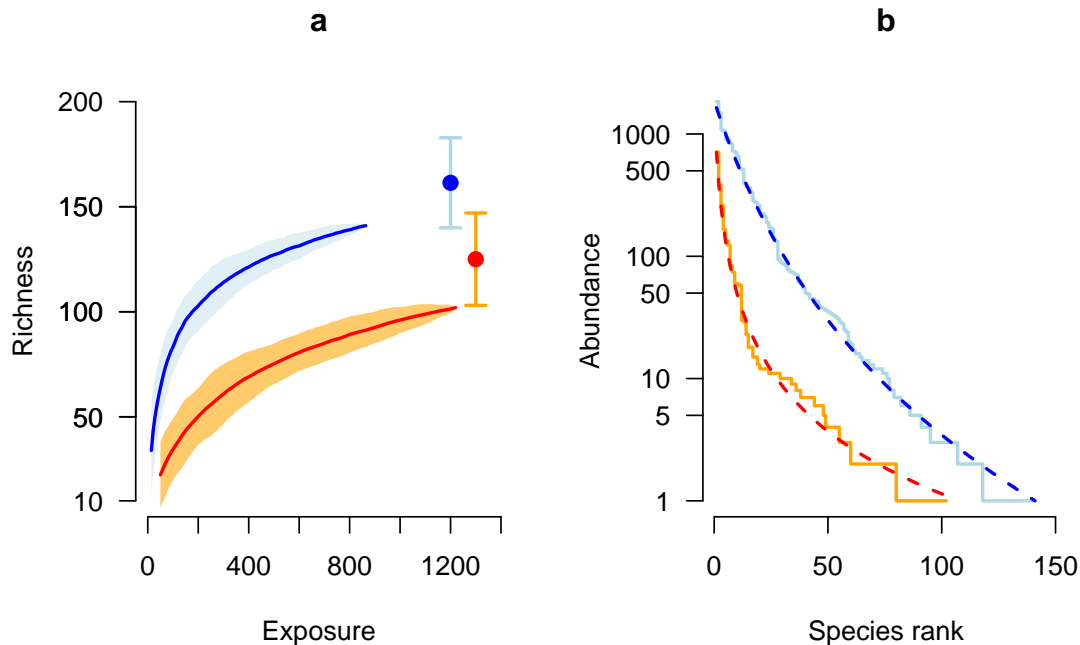


Figure 5.2: **Comparison of species richness and species relative abundance between 1989 (blue) and 2014 (orange) based on the pooled data of six malaise traps, for each year.** **a:** Species accumulation curves along with 95% intervals based on 100 random permutations of original data (data pooled within year), against cumulative exposure time (number of sampling days). Points depict Chao's estimates of richness in each year along the 95% confidence intervals. **b:** Rank abundance curves where solid lines depict data and dashed lines the fitted Zipf-Mandelbrot estimates (see also Supplementary Figure D2).

### 5.3.5 Daily abundance and richness

Total abundance models that included climatic variables outperformed models without ( $\Delta\text{DIC} = 2929.73$ ), with significant positive effects of mean day-temperature and significant negative effects of daily precipitation and wind speed ( $\text{pmf}(|z| < 0) = 0$ ). Effects of trap and day number were significant and were retained as well (see Supplementary Table D1). The coefficient for change in total daily hoverfly abundance was negative and highly significant:  $\log(\lambda_{\text{abundance}}) = -1.757$ ,  $\text{sd} = 0.022$ ,  $\text{pmf}(|z| < 0) = 0$ , implying an estimated mean loss of 82.7% (CI: 82.0-83.5) in abundance per day over a 25 year period. Seasonal trajectories of abundance for 1989 and 2014 are given in Figure 5.3a. The expected daily number of species using abundance based Chao's estimator for 1989 and 2014 are given in Figure 5.3b. Similarly to total abundance, the covariates weather, trap effects and day number were found significant and were retained (see Supplementary Table D2). Following corrections for weather and seasonal effects, the estimated daily number of species was 15.94 (CI: 14.9-16.9) in 1989 versus 2.99 (CI: 2.8-3.2) in 2014, implying an 81.2% (CI: 79.6-82.6) decrease in daily species richness.

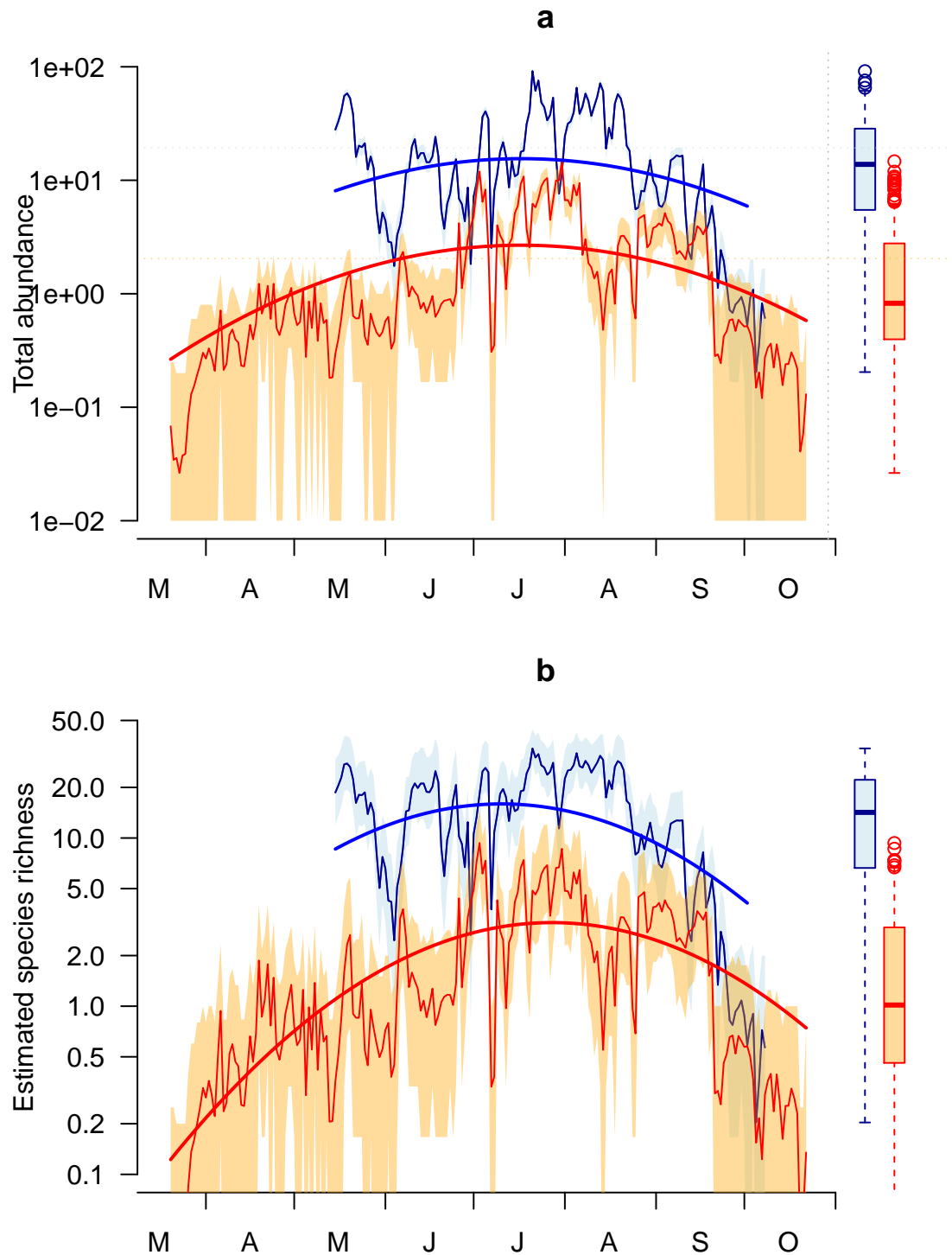


Figure 5.3: **Seasonal trajectory of estimated number of hoverfly individuals (a) and species (b) in 1989 (blue) and 2014 (red) along with 95% credible intervals. Boxplots provide the distribution of the mean daily values over the two seasons.**

### 5.3.6 Individual species persistence and decline rates

For the 141 hoverfly species caught in 1989, the probability of being caught again in 2014 increased linearly with log abundance in 1989 (Figure 5.4a). The probability of presence in the 2014 trap data (given presence in 1989) was lower than expected from a null model with a uniform per capita decline rate across species, only however for the species that were relatively abundant in 1989 (Figure 5.4a). This suggests that among species, abundance is not the sole determinant of persistence. Among species present in both years ( $n=81$ ), species densities in 2014 were within confidence levels under an expectation of uniform decline (Figure 5.4b), although changes in abundance between the years differed considerably between species. Out of the 20 most common species in 1989 ( $N>200$  trapped), two were extirpated in 2014, while the remainder were all severely reduced in numbers. Of the rarest 50 species (between 1 and 4 individuals caught over season) in 1989, most declined while a few increased in abundance; 33 species of this group were not seen in 2014, representing a decline of 66% which is a lower declining rate as compared to the average of 82.7% over all species. Out of the 21 species seen only in 2014, 18 were not abundant ( $N\leq 4$ ), suggesting a negative balance in extinction/colonization rates for both species richness and species abundance.

## 5.4 Discussion

Our analysis shows that the biomass of total flying insects of the six Malaise traps analysed presently correlates strongly to the total number of individuals of hoverflies in the samples, and as such, the decline of 75% in total flying insect biomass over a 25 year period, translates to a net loss of over 80% in total hoverfly abundance, and a 20% overall loss of richness (pooled over the traps and the seasons). However, at the daily level, both hoverfly richness and total abundance show comparable declines, at the order of 80%, indicating a strong temporal scaling in species presence. No change in the distribution of body sizes of hoverfly species between the two sampling years, eliminating the possibility of smaller species replacing larger ones (e.g. Scheper *et al.*, 2014; English *et al.*, 2018). Large declines in total flying biomass observed in the broader lowland Germany in Hallmann *et al.* (2017) could therefore be indicative of both numerical abundance and diversity of hoverflies, and possibly to the state of the diversity in other insect taxa.

The current analysis revolves around six traps, with all traps located in nutrient-rich and moist abiotic conditions close to forest-grassland borders, and surrounded by agricultural landscape. In first principle, it is unknown how representative the richness and abundance of hoverflies in these trap locations is to the broader landscape. Additionally, our analysis encompasses solely hoverflies (with  $< 5\%$  estimated share in total biomass), and not the full range of all other flying insects sampled by malaise traps. However, despite the low contribution of hoverflies to the total flying insect biomass, the remarkably high correlation between total biomass and hoverfly abundance and diversity, as well as the correspondence of local abundance to regional commonness (Ssymanck *et al.*, 2011, see Supplementary Figure D4) suggest that biomass declines can be indicative to biodiversity loss. Additionally, total flying biomass samples, as well as their regional temporal trend seem to be well represented by the presently analysed samples (see Supplementary Figure D3), suggesting that the observed declines in hoverfly diversity may well be representative for the regional trends of hoverflies.

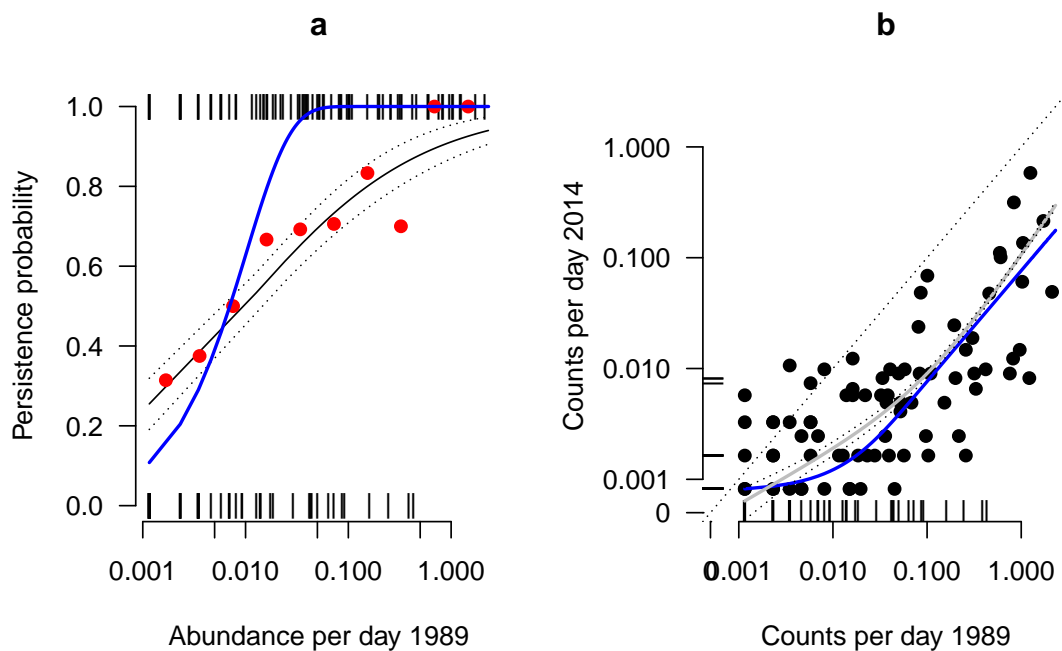


Figure 5.4: **a: Probability of species persistence in the Malaise trap data versus log abundance.** Red points depict average probabilities over ten equidistant classes of abundance (for depiction purposes only), while solid black line the fitted probabilities from a logistic regression. The blue line depicts the expected persistence probabilities calculated under a null-model with uniform rate of per capita decline across species (see methods). **b: Population sizes in 1989 versus 2014.** The solid grey line depicts a fitted third polynomial trend between the counts of the two seasons, while the blue line depicts the expected rate of decline assuming a uniform rate of per capita decline across species. Tick marks at the axes indicate the abundance of species that were only caught in 1989 or 2014.

The decline in abundance spans, with minor exceptions, across the hoverfly-species spectrum. However, declines in formerly abundant species contributed disproportionately to the decline in total abundance. In some species (e.g. *Syrirta pipiens*, *Platycheirus albimanus*) the magnitude of decline in abundance spans over two orders (-99.3% and -97.7%). Among rare species, demographic theory predicts higher extirpation rates for rare species owing to increased extinction risk due to demographic stochasticity. Surprisingly however, here extirpation of the less abundant or rare hoverfly species occurred above expected levels under a uniform per capita declining rate. Contrary, declines in species of intermediate abundance have led to higher-than-expected extirpation probabilities. None of the few species observed only in 2014 were numerically abundant, and hence they did not offset the decline in numbers by abundant species in 1989. According to Thomas (2016) and Habel & Schmitt (2018), species that intermediate between specialists and generalists, nowadays too exists as remnant and fragmented populations, are the group of species likely to have contributed most to declines in total abundance (and hence biomass Hallmann *et al.*, 2017). Contrary to specialists, that tend to naturally be rare and which are expected to have better adapted to isolation, and contrary to highly mobile generalists, the group of species of intermediate specialization and mobility are likely to have suffered most in recent decades from increasing land use intensity and fragmentation. The present results partially confirm these expectations, although also the highly abundant species seem to be affected as well. Although most conservation attention is traditionally devoted to the group of rare species, our results emphasize that it is not the group of the rarest species that is disproportionately at peril in the overall loss of the insect community.

While the overall species richness of hoverflies has declined less as compared to the total abundance of hoverflies (20% less richness versus 80% decreased abundance) when considering the entire season, daily species richness has declined just as much as total daily abundance, revealing a strong temporal scaling in diversity loss. While the volume of ecological functions is proportional to the richness (Oliver *et al.*, 2015), the bulk of ecosystem functioning is mostly governed by the abundance of species (Winfree *et al.*, 2015). The severe drop in both daily richness and abundance during the vegetative season, suggest that both the diversity as well as quantity of the ecological functions that hoverflies perform (e.g. pollination, predation) have been severely deteriorated.

A number of causes are known to affect hoverflies and other insects. Climate change, habitat loss, fragmentation and degradation, and effects of agricultural intensification such as eutrophication and pesticides, are some the most commonly cited causes (Conrad *et al.*, 2006; Ollerton *et al.*, 2014; Schweiger *et al.*, 2007; Fox *et al.*, 2014). In the present study, weather effects such as increased precipitation in 2014 were not sufficient to explain the approximately 80% decline in hoverfly abundance and richness, while temperature and wind were at comparable levels between the two years, explaining only day to day variation in trap catches. Therefore, there is little evidence that climate change may have played a central role in hoverfly declines. However, the variables used presently do not cover the full range of climatic variables that might affect hoverflies, such as extreme events (e.g. Lister & Garcia, 2018), and more research is due. Hoverflies are known to require a diverse landscape (Meyer *et al.*, 2009; Villa *et al.*, 2016; Moquet *et al.*, 2018). Many hoverfly species prefer habitat mosaics where spatially adult habitats and larval habitats are not widely separated, such as grassland - woodland edges or hedgerows (Ssymank, 1991, 2001). Local richness is expected to respond to availability of habitat for both larvae and

adult habitat (Meyer *et al.*, 2009; Villa *et al.*, 2016; Moquet *et al.*, 2018), while densities of hoverflies are likely to depend on the availability of resources for adults (pollen en nectar), and larvae (e.g. aphids Meyer *et al.*, 2009; Villa *et al.*, 2016). On the basis of vegetative assessments, trap locations showed improved vegetation structure and increased plant diversity over time, however, flowering plant coverage was not assessed, so that it remains hard to infer whether adult energy requirements are met at the investigated locations. Ellenberg index values for pH and Nitrogen did not show a great variation or consistent change between the two sampling years, suggesting that eutrophication is not evident in the plant communities of the Wahnbachtal. Hence, there are no obvious signs that might hint at a severe vegetative degradation of adult habitat in these locations, able to explain the broad decline observed.

## 5.5 Conclusion

The broad decline in insects witnessed in Germany (Hallmann *et al.*, 2017) suggests that insect communities have been decimated in recent decades. Our analysis of hoverfly communities confirms that declines occur across species, with increased stochastic extirpation particularly for species of intermediate abundance. As hoverflies are a relatively rich and diverse taxon (in terms of habitat requirements), the observed declines across the species (most losers, hardly any winners) may suggest a common and indiscriminate factor to be responsible for the declines, such as the presence of pesticides in the surroundings (e.g. Rundlöf *et al.*, 2015), or other large scale environmental changes. The ramifications of abundance loss for ecosystem functioning and ecosystem services need to be investigated. The severe drop in numbers and richness is bound to have consequences for plants that depend on pollination for their reproduction (Biesmeijer *et al.*, 2006), and as a food resource for higher order taxa (Schrauth & Wink, 2018; Bowler *et al.*, 2019; Møller, 2019). Crop pollination and pest suppression by hoverflies (Chambers & Adams, 1986; Rader *et al.*, 2016) are likely to be in jeopardy too. Trait based analysis of current trends with respect to ecological requirements of the species (e.g. degree of specialization, life history characteristics), in combination with measurable changes in environmental conditions (e.g. climate, plant diversity, pollution) might provide the basis for such an analysis. Both monitoring and conservation initiatives need to be established in order to further assess causes, consequences, and to provide guidance with developing mitigation strategies,





## 6. Synthesis

Malaise trap in German nature reserve. Photo credit: *Martin Sorg*

Caspar A. Hallmann

Biological diversity is threatened with changes in the landscape related to agricultural intensification being the largest contributor to species declines in Europe (WWF International, 2018). Despite a body of research and wealth of information, we are still only beginning to comprehend the scale of biodiversity loss, and to understand which are the key drivers, and what are the ramifications. This lagging knowledge hampers effective conservation measures, and despite ambitious targets for the protection and restoration of biodiversity at national and international scale, over the recent decades we have witnessed loss of species, biotic homogenization, and wildlife communities dominated by generalist species, and more recently (Habel & Schmitt, 2018), a large drop in abundance of formerly common species. In light of these observations, this dissertation provides insights into the scale of biodiversity loss in modern human-dominated landscape (chapters 3-5), and attempts to uncover and compare drivers and mechanisms responsible for the observed trends in birds and insects in recent years (Chapters 2, 3 and 5). In this synthesis, I provide an overview of the most important findings of this thesis, and discuss these in relation to current state of knowledge on the extent of biodiversity loss, and on the potential causes and consequences thereof. I conclude by providing an overview of knowledge gaps and future research priorities, and provide an outlook for biodiversity conservation in modern agricultural landscapes.



## 6.1 Biodiversity conservation and agro-chemicals

Global declines in biodiversity have provoked the need to uncover ecological determinants of the persistence and abundance of species. Changes in land use, agricultural intensification, and climate, as well as invasive species, have been postulated as the major driver of current anthropogenic biodiversity loss in the period after the second world war (WWF International, 2018, Chapter 1). Among aspects of agricultural intensification, increased input of synthetic fertilizers and pesticides have been proposed as major contributing factors to bird, insect and plant declines (Chamberlain & Fuller, 2000; Donald *et al.*, 2001; Boatman *et al.*, 2004; Tschardtke *et al.*, 2005; Geiger *et al.*, 2010; Tschardtke *et al.*, 2012; Mineau & Whiteside, 2013). Concerns with respect to the negative effects of pesticides to biodiversity are not recent, but date back since the pioneering work of Rachel Carson (Carson, 1962; Krebs *et al.*, 1999), and the negative effects of now-banned compounds such as organophosphates.

In the Netherlands, pesticide usage is the highest among European countries, with on average total of 26745 kg/year of active ingredients applied in agriculture in the period 2005-2016 (Nefyto, 2017). Neonicotinoids, broadly applied systemic insecticides over the past 25 years, are known to affect wild-bee communities in arable land (e.g. Rundlöf *et al.*, 2015), and are evidenced to diffuse, persist, and accumulate in both terrestrial (Goulson, 2013; Humann-Guillemintot *et al.*, 2019a) and aquatic (Dutch Pesticides Atlas, 2009) environments. In Switzerland for example, a recent study reported 93% of organic soils -where no pesticides are applied- to be contaminated with at least one neonicotinoid compound (Humann-Guillemintot *et al.*, 2019a). Owing to their relatively high toxicity to insects (Pisa *et al.*, 2015), neonicotinoids have been postulated as a threat to pollinators and biodiversity in general (Goulson, 2013; Gibbons *et al.*, 2015; Gilburn *et al.*, 2015; Pisa *et al.*, 2015; Rundlöf *et al.*, 2015; Forister *et al.*, 2016; Wood & Goulson, 2017, Chapter 2). Indeed, water and soil contamination has been shown to affect wildlife communities either directly (van Dijk *et al.*, 2013; Gilburn *et al.*, 2015; Gibbons *et al.*, 2015), or indirectly through the trophic chain (Douglas *et al.*, 2015, Chapter 2). In the Netherlands, lowered population trends among 15 insectivorous passerine birds coincided in time and space with imidacloprid contamination in surface waters (Chapter 2), and explained bird trends better as compared to other aspects of land-use changes.

Because neonicotinoids were thought to be selective, i.e. attacking the central nervous system of insects only, direct lethal effects were not envisaged. Rather, declines in the prey base were deemed a more likely explanation for the lowered population trends of the bird species investigated. However, reports of both direct and indirect accumulation of neonicotinoids in birds have been issued. In France for example, carcass analysis of four granivorous bird species (*Perdix perdix*, *Columba palumbus*, *C. livia*, *C. oenas*) suggested imidacloprid to be the lethal cause in over 70% of the cases (Millot *et al.*, 2017). Humann-Guillemintot *et al.* (2019b) showed the presence of neonicotinoids in house sparrow (*Passer domesticus*) feathers to be widespread in Switzerland. In two other studies, accumulation of neonicotinoid compounds in feathers and blood of top predators (*Bubo bubo*, *Pernis apivorus*) were reported (Byholm *et al.*, 2018; Taliansky-Chamudis *et al.*, 2017). Finally, a recent contribution showed that neonicotinoids may affect migratory abilities, body mass and reproduction of white-crowned sparrows (*Zonotrichia leucophrys* Eng *et al.*, 2017), while experimentally, ingestion of treated seed showed lethal and sub-lethal effects on red-legged partridges (*Alectoris rufa* Lopez-Antia *et al.*, 2015). As such, multiple

mechanisms may be at play by which neonicotinoids affect avian species. Ingestion of these compounds by either treated seed, contaminated water or prey may be an additionally important pathway, despite the common belief that these compounds are less detrimental to mammals and birds than to insects (Tomizawa & Casida, 2005).

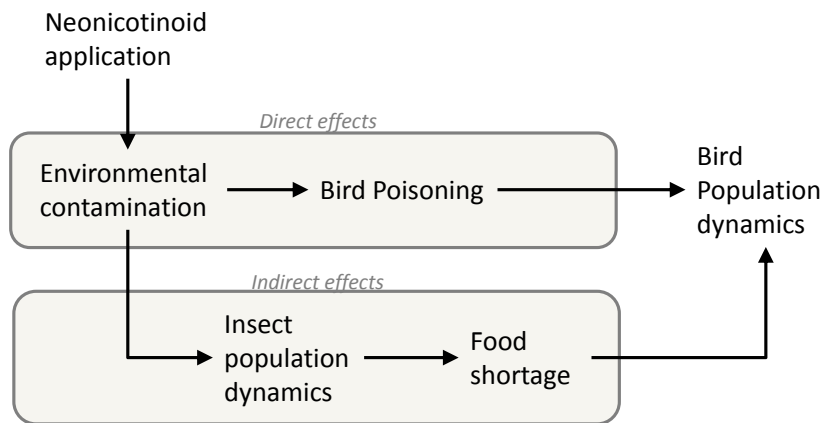


Figure 6.1: Schematic diagram of direct and indirect effects of neonicotinoid environmental contamination on bird population dynamics. Following application, neonicotinoids may affect bird population dynamics in two ways: A direct route by ingestion of treated seed, or contaminated prey, and subsequent poisoning (e.g. Millot *et al.*, 2017; Byholm *et al.*, 2018), and an indirect route, by which neonicotinoid leaching into soil and water in the environment negatively affects insect populations, and causes a food shortage for birds.

Evidence for the case of neonicotinoids affecting birds through trophic cascades, i.e. food deprivation, (Chapter 2) can be substantiated more, by integrating over all ecological processes involved. While correlative approaches (Chapter 2 van Dijk *et al.*, 2013; Gilburn *et al.*, 2015) allow the quick assessment of the potential of neonicotinoid effects in the environment, they are generally not regarded as proof of causality. A causal basis on which neonicotinoids affect the birds through a diminished insect prey base and food limitation, requires an integrated assessment of all the steps involved, while at the same time controlling for possible direct effects, such as poisoning. A schematic overview of these steps is given in Figure 6.1 include:

1. Contamination of the environment to the extent it may be expected to affect insect communities,
2. Declines in insect communities through direct (e.g. mortality, impaired reproduction),
3. Insect population declines of sufficient magnitude to cause food deprivation for birds,
4. Reduced avian demographic performance, and finally
5. Insectivorous bird population decline.

A study looking at these steps collectively has not been carried out as of yet, but is underway at the Radboud University in the Netherlands. However, evidence so far confirms steps 1, 3 and 5, namely contamination (van Dijk *et al.*, 2013, Chapter 2), evidence for insect decline in contaminated areas (van Dijk *et al.*, 2013; Easton & Goulson,

2013; Gilburn *et al.*, 2015; Rundlöf *et al.*, 2015), and subsequently lowered population growth rates of insectivorous birds (Chapter 2; Stanton *et al.*, 2018; Bowler *et al.*, 2019; Møller, 2019). So can neonicotinoid-caused food deprivation explain lowered demographic performance of avian populations? The observed declines in abundance of various insect species (Chapters 4-5), as well as their biomass (Chapter 3, see below), have not been linked to neonicotinoid usage in this dissertation. Lack of appropriate data inhibits a thorough analysis at this point for the presented insect data sets. This forms a serious gap in the knowledge and is one that needs to be investigated with high priority. It calls for a rigorous integral monitoring of application and contamination of natural areas and waterways with agrochemicals, which is currently lacking in most parts of the world.

The demographic mechanisms (step 4) mediating neonicotinoid contamination and lowered avian trends are likewise understudied. Lowered prey base may affect demographic rates such as survival of adults and chicks, reproductive success, or the occupation of territories (in the case bird species prospect for sites based on prey availability cues). The most clearly documented relation between pesticides and demographic effects in birds, are the studies on the partridge (*Perdix perdix* Rands, 1985; Potts & Aebischer, 1991; Aebischer & Ewald, 2004), for which negative responses were observed in reproduction mediated by declines in insect prey base. Other species that showed an apparent negative response of demographic traits to pesticides include the yellowhammer (*Emberiza citrinella*, Morris *et al.*, 2005; Hart *et al.*, 2006), and the corn bunting (*Miliaria calandra*, Brickle *et al.*, 2000; Boatman *et al.*, 2004). To date however, no study has demonstrated a demographic response of birds to neonicotinoids in the environment.

Furthermore, accounting for confounding factors, such as other aspects of land use intensification, or confounding mechanisms, such as the effects of direct exposure of organisms to neonicotinoids, remains of paramount importance in assessing empirically the effects of these compounds on exposed animals. Nevertheless, sufficient prey availability is essential in maintaining healthy insectivorous bird populations, and arguably food deprivation in contaminated areas remains one of the most obvious mechanisms in affecting bird populations, and particularly so in farmland. The severe decline in insects that have recently been reported (Dirzo *et al.*, 2014, Chapters 3-5) in nature reserves in between farmland corroborates this hypothesis, although knowledge on the state of insects is usually rather limited.

## 6.2 The state of insects

There have been increasing concerns with respect to the state of insects (Thomas *et al.*, 2004; Shortall *et al.*, 2009; Dirzo *et al.*, 2014; Fox *et al.*, 2014; Habel *et al.*, 2016; Habel & Schmitt, 2018) and in particular pollinators (Potts *et al.*, 2010), as well as their interaction with plants (Biesmeijer *et al.*, 2006; Scheper *et al.*, 2014). Although butterflies and moths are thought to be appropriate indicator species (Thomas *et al.*, 2004; Hambler & Speight, 2004), we have been uncertain to what extent the trends of these species are representative for the broader insect community. (Dirzo *et al.*, 2014) found for example that lepidopterans are in decline but less so than all other insect groups for which data are available. In general, we have a rather poor understanding of the state of entomofauna for most taxa, and for most parts in the world (Sánchez-Bayo & Wyckhuys, 2019). The decline of more than 75% in total flying insect biomass over 27 years in German lowland nature reserves (Chapter 3)

as well as in specific insect groups (Chapters 4-5) however signals that declines in insects possibly extent well beyond butterflies and moths. Together with other results (e.g. Conrad *et al.*, 2006; Kuussaari *et al.*, 2007; Brooks *et al.*, 2012; Fox *et al.*, 2014; Habel *et al.*, 2016; Lister & Garcia, 2018), insect declines have been well discussed among academics, media, and policy makers. Yet, it is evident that the number of published studies on insect trends and distribution originate in Europe and North America (Sánchez-Bayo & Wyckhuys, 2019; Thomas *et al.*, 2019), and great uncertainties exist about the state of insects in other parts of the world. Moreover, not all species are in decline (Shortall *et al.*, 2009; Bell *et al.*, 2015; Termaat *et al.*, 2015; Herrera, 2019). Dragonflies for example have been in the rise in recent decades (Termaat *et al.*, 2015) although this increase has halted in the last few years). (Shortall *et al.*, 2009) found declines in insect biomass in the UK in only one of the four areas with long-term trends on insect biomass, although the other three areas were likely already impoverished prior to the onset of the collection of data. Within taxa, great variation between species is also present (e.g. Chapter 4), and while most species among beetles and macro-moths were in decline, some species were increasing over the same period. In pristine areas in Spain, insects appear not to be affected (Herrera, 2019).

### 6.2.1 Causes of insect decline

With novel agronomic measures posing new and additional threats to biodiversity (e.g. application of neonicotinoids), it becomes increasingly challenging to tease apart the relative role of each hypothesized driver of insect decline. Nonetheless, substantiated by a large body of evidence, we argued that factors related to agricultural intensification form the prime suspect in the present insect decline (Chapter 3), although it is still unclear which of the mechanisms are responsible. There are broadly two ways by which insect communities may be affected by surrounding agriculture: through influences of agriculture on the populations in the nature reserves by contamination (nutrients/pesticides), and secondly, through inhibited dispersal of insects into inhospitable areas. Pesticide contamination outside farmed land was shown near bird monitoring plots in the Netherlands (Chapter 2) and elsewhere (e.g. Switzerland Main *et al.*, 2014; Humann-Guillemot *et al.*, 2019a). Detection of neonicotinoids have also been made in wild flowering plant in strips near cropped areas (Botías *et al.*, 2015). The diffusion and persistence of these compounds in the environment is now beyond doubt, suggesting that environmental degradation through pollution to be a likely cause of insect decline. However, insects dispersing into the agricultural matrix may equally affect insect populations within the reserves. In Sweden, for example, wild-bee numbers were substantially lowered in fields experimentally applied with neonicotinoid pesticides (Rundlöf *et al.*, 2015). As many of these wild pollinators are attracted by the flowering crops, or their pests (e.g. in the case of natural pest control agents such as the hoverflies, Chapter 5), nature reserves may be drained of insect species that disperse into highly unsuitable habitat of intense land use. In turn, this may render farmland an ecological trap for many of those species (Battin, 2004), with source sink dynamics (i.e. reserves being the sources, and farmland being the sinks; Pulliam, 1988) as the regulating process of insect population decline in the reserves.

### 6.2.2 Ecological ramifications of insect decline

The decline of insect populations is expected to affect ecosystem functioning, such as plant pollination and food provisioning to higher order taxa. Much of the consequences for

ecosystem functioning will depend on how declines are shared among common and rare species, and their ecological role in the ecosystem. In principle, while reduction of insect biomass at such proportions cannot be envisaged without numerical declines of abundant species, essentially reshaping the insect community, biomass itself does not reveal how insect diversity is affected, and which ecosystem functions are affected and to what degree. However, as **Chapter 5** describes, the 75% decline in total flying biomass is paralleled by an isometric decline in daily total abundance and richness of hoverflies, suggesting that insect biomass declines appear to be indicative to insect diversity. Hoverflies are a diverse group of insects and are naturally involved in a great variety of ecosystem processes (Sommaggio, 1999). The decline in almost all species of hoverflies therefore suggests the impairment of various ecological functions in the studied areas, such as pollination, predation, and providing a food source for higher trophic levels.

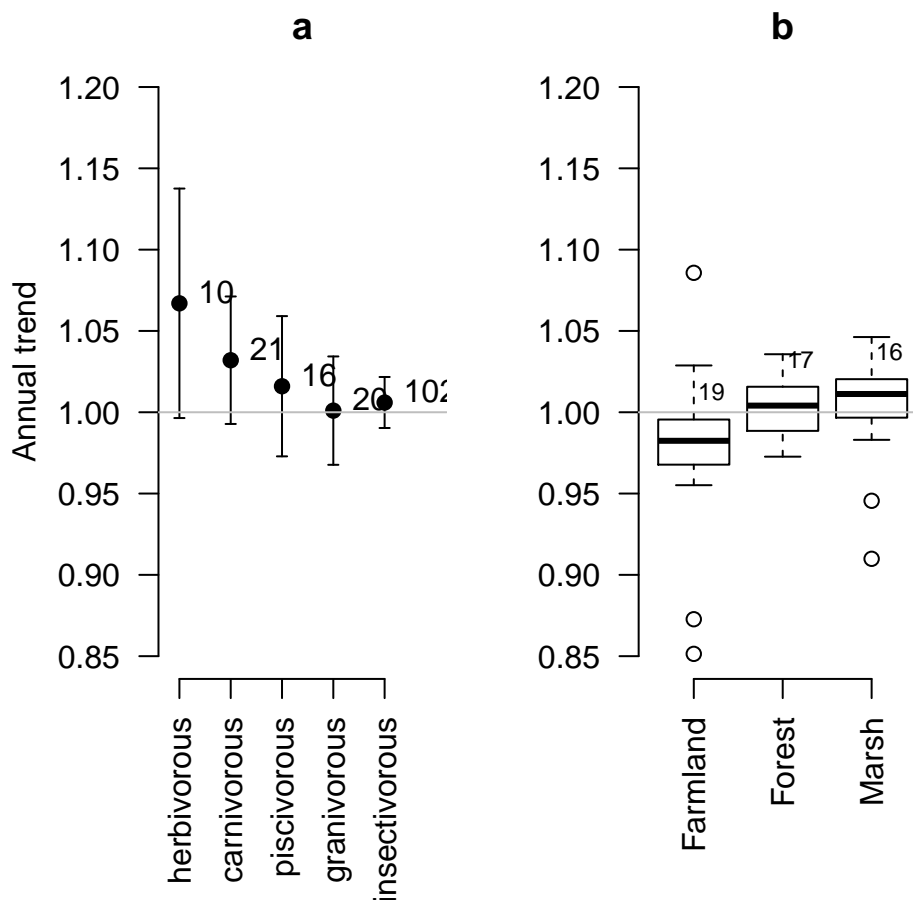


Figure 6.2: Average trends (annual multiplication factor  $\pm$  95% confidence levels) of bird species in the Netherlands for various diet types (a; Data from van Turnhout *et al.* (2010), Table 3, for the period 1990-2005) and insectivorous birds alone along three main habitat types (b; trends calculated based on indices from CBS (2018b) for the period 1990-2017). Depicted numbers indicate number of species involved in the calculations.

Long term studies on butterflies and moths (Warren *et al.*, 2001; Fox *et al.*, 2014; Habel *et al.*, 2016; Inger *et al.*, 2015; Habel *et al.*, 2016; Thomas, 2016), have shown that rare

species, specialists, and species with restricted distributions are usually less resilient to environmental changes (e.g. land use changes, climatic changes), and hence were first to leave to local communities. In the present cases (Chapters 4 and 5), the bulk of the losses appear to be driven by both higher than expected extirpation probabilities of moderately common species (hoverflies), as well as by declines in abundance of the formerly most common species (hoverflies, moths and beetles). Elsewhere, declines of common species of e.g. butterflies and moths in either distribution or abundance are reported as well (Conrad *et al.*, 2006; Van Dyck *et al.*, 2009; Wepprich *et al.*, 2019). Together, these results possibly point to a new phase in the biodiversity crisis, one in which the struggle to maintain biodiversity will have to integrate both targeted species conservation (as is the case for rare and specialized species) as well as keeping the common species common. As generalists dominate the communities numerically, declines in these species are expected to lead to much larger losses in total abundance and biomass (Chapters 3-5) as compared to the declines of less abundant species. As a consequence, the total amount of ecosystem functioning (in terms of energy flowing through a trophic level) can be expected to be reduced in similar proportions.

A most notable effect of severe insect decline would be a knock down of food resources for species in higher-order trophic levels such as birds and bats. Indeed, insectivorous birds seem to be doing worse than other avian diet types in Europe (Schrauth & Wink, 2018; Bowler *et al.*, 2019; Møller, 2019) and North America (Nebel *et al.*, 2010). In the Netherlands, insectivorous bird trends are on average stable, but show great variation among species, and are lower as compared to for example phytophagous or carnivorous species (van Turnhout *et al.*, 2010, Figure 6.2a). Yet, these results are at national level, ignoring any habitat specific variation in species trends (Gregory *et al.*, 2005). For insectivorous bird species alone for example, published indices (CBS, 2018b) based on data from Sovon, the Dutch centre for Field Ornithology, show on average lower trends of species in farmland as compared to species in forest or marshland (Figure 6.2b). Clearly, this calls for additional in depth studies to examine the role of insect-abundance and bird population dynamics, specifically integrating interactions between habitat type and main diet type.

### 6.3 Concluding remarks and future outlook

The results of this dissertation have shown that neonicotinoid insecticide contamination may affect bird population dynamics of insectivorous species, possibly through a lowering of insect prey base. Large scale drops in insect biomass, abundance and diversity in nature reserves in Germany and the Netherlands underline a possible role of food shortage to higher trophic levels such as birds, and may further hint at disruptions of multiple other ecological functions. The observation that formerly abundant species have also been decimated in recent decades is alarming, as it suggests that large scale factors must be involved, leading to impairment of ecosystem functioning. Conservation efforts have overlooked common and widespread species in the past, and it is evident current conservation strategies should be adopted in order to include those species as well. Birdlife Europe has for example currently adopted "keeping common birds common" as objective in bird conservation strategies (<https://www.birdlife.org/worldwide/partnership/our-vision>).

Results in this dissertation support the concerns with respect to a global biodiversity crisis, and the role of contemporary land use in declining biodiversity. Fortunately, public

awareness has increased in the last few years, and efforts to combat biodiversity declines are under way. For example, in the Netherlands, new initiatives such as the *Deltaplan Biodiversiteit* that integrate multiple stakeholders (from farmers to banks) are a very promising tool in this respect. In Germany, the "Action Program for Insect Protection" was established by the ministry for the environment, nature protection and nuclear safety (<https://www.bmu.de/insektenschutz/>), while at the level of the European Union, programs to monitor and mitigate pollinator decline have been initiated (Underwood *et al.*, 2017, [http://ec.europa.eu/environment/nature/conservation/species/pollinators/index\\_en.html](http://ec.europa.eu/environment/nature/conservation/species/pollinators/index_en.html)). Furthermore, the ban of several neonicotinoid pesticide compounds in the European Union in open field arable land is considered beneficial to many species in farmland (Wood & Goulson, 2017). These actions are clearly a step the right direction, and show willingness and commitment of both the public and at policy level to mitigate the biodiversity crisis. While severe knowledge gaps still exist, such as the exact causes and ramifications of insect decline, these should not justify inaction in await for better data and more research. Rather, conservation measures should be deployed where they are believed to be beneficial (better grassland management, support nature-inclusive farming practices), and practices perceived to be detrimental to insects should be avoided where possible (i.e. abandoning prophylactic pest management).



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Foraging female Common sparrow *Passer domesticus*. Photo credit: Jouke Altenburg

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# Appendix A: Supplementary material for Chapter 2

In this Supplementary Information we present all details of our data and analyses. In the Supplementary Data section, we provide a description of the selected bird species and the data used to calculate their local population trends. In addition, we describe the database of imidacloprid concentrations in Dutch surface water and finally data on other variables measuring agricultural intensification. In the Supplementary Methods section we explain how we related imidacloprid concentrations to bird monitoring plots spatially, and provide a detailed overview of the regression modelling details.

## Supplementary Data

### Bird species selection

We selected all 15 passerine bird species (see Supplementary Table A1) that meet the following requirements: they are common to the Dutch agricultural landscape, they forage in habitats most likely to be exposed to imidacloprid contamination (farmland, grassland, farms, reed and shrubs), for which data exists with sufficient spatial coverage across the Netherlands, and whose food source during the breeding season consists mainly of small invertebrates.

We selected bird species that feed on small invertebrates, as these invertebrates are known to suffer from elevated neonicotinoid concentrations (van Dijk *et al.*, 2013; Easton & Goulson, 2013; Roessink *et al.*, 2013). Our list of species includes two resident, five short-distance migratory species, and eight long-distance migratory species. According to national trend estimates (Statistics Netherlands 2013), four of the species showed increasing trends, four showed stable trends and seven showed a negative trend in the period 1990-2005 (see Supplementary Table A1).

### Bird population data

We derived local population trends for the 15 selected insectivorous farmland passerines species using long term breeding bird data from the Dutch Common Breeding Bird Monitoring Scheme, which is a standardized (Bibby *et al.*, 1992; van Dijk, 2004) monitoring scheme maintained and coordinated by Sovon, Dutch Centre for Field Ornithology, in collaboration with Statistics Netherlands (van Turnhout *et al.*, 2010). Data originating from these monitoring plots are generally considered to be adequately representative and reliable for population trend estimation (Bibby *et al.*, 1992) and have contributed in the past to many large scale studies investigating for example climate effects (Gregory *et al.*, 2005; van Turnhout *et al.*, 2007, 2010; Devictor *et al.*, 2012; Kampichler *et al.*, 2012). The bird monitoring scheme is based on intensive territory mapping of all breeding birds present at fixed study plots, where multiple visits (5-10) per breeding season (March-July) are used to determine the number of territories for each species. The number of territories is determined by species-specific interpretation criteria, which are formulated based on behavior observed (e.g. song, pair bond, display, alarm, nests), detection probabilities (embodied by a minimum number of observations required per species) and timing of observations (to exclude observations of non-breeding migrants early and late in the season). The scheme has been running in the Netherlands since 1984, and is effectuated by trained volunteers and professional observers. Monitoring plots range in size between 10 ha and 1000 ha. The number of study plots increased from around 300 per year in the mid-1980s to 1900 at the end of the study period. For the analysis, we ignored data from plots with less than three years of non-zero territory counts for a given species to avoid using data on species that only rarely occupy a given plot. In addition, we ignored territory information from plots > 5 km from imidacloprid measurement points in order to avoid basing inference on distant interpolations. In total, 354 monitoring plots (17-200 for individual species, Supplementary Figure A2) and 1459 species and plot-specific estimates of population trend were used to investigate relationships with imidacloprid concentrations.

### Imidacloprid data

We used imidacloprid measurements located throughout the Netherlands (Supplementary Figure A1) from the Dutch Atlas of Pesticides in Surface Water (Dutch Pesticides Atlas 2009). These data originate from a national monitoring program on pesticides in Dutch surface water, and is mandated by the Dutch water-board authorities, Leiden University and the Board for the Authorisation of Plant Protection Products and Biocides (Ctgb). The dataset was previously used by van Dijk *et al.* (2013) in relation to macroinvertebrate abundances. The dataset encompasses in total 9037 measurements made by the Dutch water-board authorities in the period 2003-2009. Records of this dataset were included in the analysis if they represented a measured concentration (31% of the data), or if they represented a "limit of concentration" not exceeding 10 ng/l (another 29% of the data). In records concerning reporting limits beyond 10 ng/l, we deemed uncertainty in imidacloprid concentrations too high, because in those cases the actual imidacloprid concentration could be anything between zero and the high value of those reporting limits. Consequently, we ignored 3616 records (40%) from the total dataset. In order to obtain a set of spatial points resembling an overall picture of water contamination during the breeding season over the period 2003-2009, we used all records made during March-September (which covers the total breeding and post-fledging periods over all species considered). In

total, 3947 measurements were used to obtain averaged log-concentrations at 555 unique sampling locations (see Supplementary Figure A1), mean number of measurements per location=7.11, sd=5.71, range=1-31).

We interpolated the average log-concentrations over a fine (250 meter resolution) grid using universal kriging with external drift (third degree polynomial of the spatial coordinates (Cressie, 1993, see Chapter 2: Figure 1a). Spatial dependence between concentrations was specified by a classical mattern variogram model fitted to the semivariance data (see Supplementary Figure A3a, variogram parameters: nugget=0.1901, sill=1.6989, range=13.2 km). These results suggest that pairs of concentrations can be spatially correlated at distances over 10 km. This spatial correlation likely reflects both a spatially clumped usage of imidacloprid, but partly also that the Netherlands has a well-connected water-infrastructure acting as a dispersal vector. Averaging of imidacloprid concentrations over years prior to interpolation was justified by noting a high between-year correlation of concentrations at the water sampling locations (see Supplementary Figure A3b), suggesting that locally, imidacloprid concentrations vary little from year to year. Finally, for each bird monitoring plot, at a distance <5 km from a measurement location, we averaged the interpolated concentrations for all grid-cells whose centroid fell within the monitoring plot boundaries.

### **Additional landscape variables**

We obtained information on surface of rural, cropped (maize and winter cereals), fallow and natural habitat (e.g. marshes, reed beds, heathlands, forests) for each municipality in the Netherlands, as well as on the application of Nitrogen fertilization (N in kg/ha Statistics Netherlands, 2013). These variables have been put forward as likely landscape changes known to affect farmland birds. Additionally, we obtained information on area of horticulture (bulb production) and greenhouses. Here, relatively higher amounts of neonicotinoids are used, hence changes in these variables may confound imidacloprid usage. Cropping and fallow land data (including bulbs and greenhouses) are collected by means of questionnaires to all farm-owners in a given municipality, employed by the municipality authorities under supervision of the Ministry of Economic Affairs, Agriculture and Innovation. Urban and natural habitat data is extracted from Dutch national land-use maps, which in turn are composed by aerial photographs and digital information system databases. Finally, data on application of fertilizers is composed by Statistics Netherlands (2013), by combining stocking densities and per capita production of faeces. Datasets for maize, winter-cereals, fallow land, bulbs and Nitrogen were available for the years 1995 and 2007, while for area of natural habitat, urban and greenhouses in years 1996 and 2006. As a measure of change, we calculated for each variable the difference in proportional surface coverage between the two successive time periods. To pair the measured change-variables to bird monitoring data we superimposed the centroid of the monitoring plots over the municipalities map. In most cases, monitoring plots were completely contained within single municipalities.

### **Supplementary Methods**

In order to investigate the effects of imidacloprid residues in the environment on the population trends of the bird species, we regressed plot- and species-specific intrinsic rates

of increase (trends) against the plot-specific average interpolated log-concentrations of imidacloprid, both for species separately and over all species pooled. We used linear mixed models (Pinheiro and Bates 2000) to relate population trends to interpolated imidacloprid concentrations when pooling over all species, and simple linear models when analysing per species separately. Plot- and species-specific intrinsic rates of increase were calculated as the slope of territory counts to year of sampling (i.e. a continuous trend) using Generalized Linear Models with a Poisson error structure and a log link. In the mixed effects models (all species pooled), besides a fixed effect for imidacloprid concentrations, we considered species intercept and slope to imidacloprid as random effects. However, as the random slope to imidacloprid concentrations for each species accounted for an insignificant amount of variance ( $sd=0.0070$ ) compared to the intercept ( $sd=0.0375$ ), we used the more parsimonious model without the random slope effect. The mixed effects models were solved using maximum likelihood estimation (Pinheiro & Bates, 2000). Tests of the fixed effect slope coefficient for log-imidacloprid in the mixed models was assessed using t-statistic as well as likelihood ratio test.

We examined the relationship of the population trends with the log of the imidacloprid concentrations for each species separately using weighted least squares. Trends per plot were weighted by the mean number of territories of the plot (over the years in which the plot was monitored) in order to avoid a high influence of demographic stochasticity of small populations.

As our maximum-distance between monitoring plot and imidacloprid sample was set to 5 km (Supplementary Data), we investigated a wide range of cut-off values, varying from 1 km to 25 km, to assess whether the choice for a particular cut-off value might affect our conclusions. Setting the cut-off distance to 1, 5 or 25 km resulted in the inclusion of 7%, 37% and 99% of the bird population data, respectively (see Supplementary Figure A5a). As is to be expected, when monitoring plots at larger distances were included in the analyses, the noise in the data increased, and the effect coefficient decreased in magnitude (see Supplementary Figure A5b). However, regardless of the cutoff distance the effect of imidacloprid remained negative and strongly significantly so ( $P < 0.00001$ ). This shows that the results and conclusion about the statistical effect of imidacloprid are robust and independent of the chosen cut-off distance.

In order to preclude that interpolated imidacloprid concentrations reflect a spatial pattern of local farmland bird declines that developed before the introduction of imidacloprid in the Netherlands, we regressed average logimidacloprid concentrations as measured during 2003-2009, to the farmland bird trends in the 1984-1995 period (i.e. before imidacloprid application), using (i) only plots that provide data in both time periods (see Chapter 2 and Supplementary Figure A6) and (ii) all available plot- and species-specific trend estimates during the 1984-1995 period. Using all available data, local trends of farmland bird populations in the 1984-1995 period did not relate to imidacloprid residues in the 2003-2009 (LMER:  $df = 1288$ ,  $t = -1.56$ ,  $P = 0.11$ ).

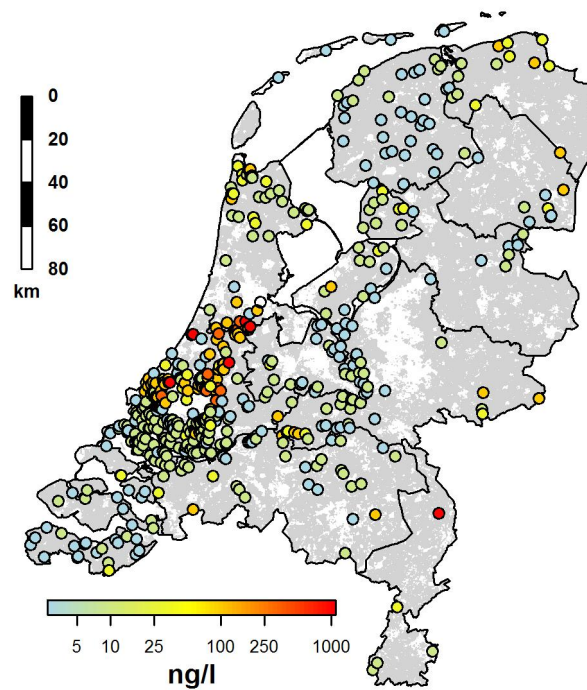
We compared the relative effect of imidacloprid versus the effects of land-use changes related to agricultural intensification in the Netherlands, by including the additional variables in a multiple mixed effects model (with species intercept as a random effect). We used F-tests based on single term deletions of the full mixed effects model (Chapter 2: Figure 2a) to assess the relative explanatory power of the variables.

All computations were carried out in the R environment for statistical computing R

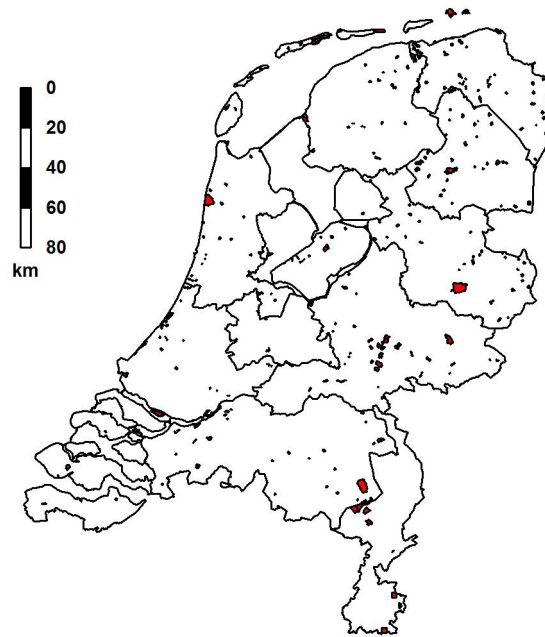
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Core Team (2015b) with the aid of packages `gstat` (Pebesma, 2004) and `nlme` (Pinheiro *et al.*, 2013).

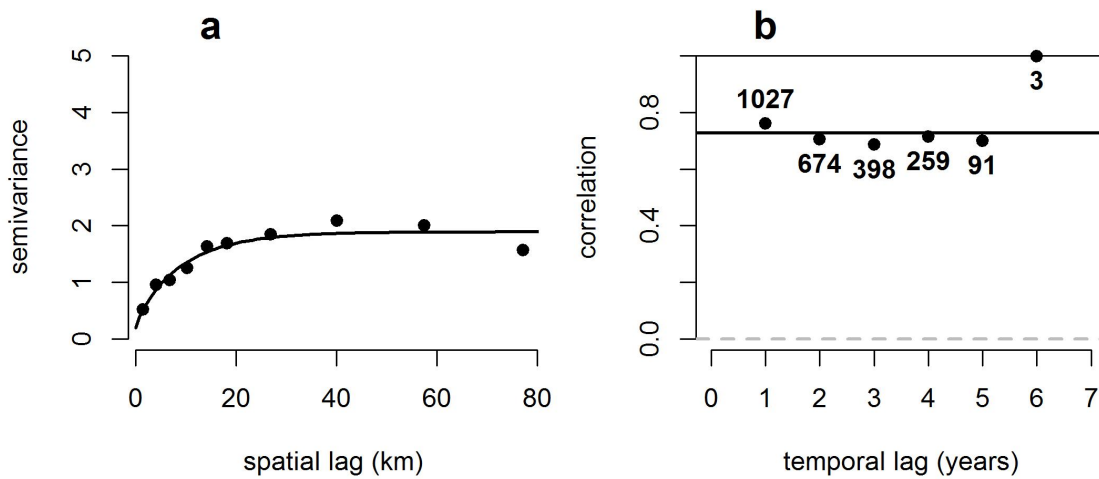
## Supplementary Figures



Supplementary Figure A1: Distribution of the 555 averages of imidacloprid measurements over the period 2003-2009, as used in the main analysis. Data:(van Dijk *et al.*, 2013; Dutch Pesticides Atlas, 2009)

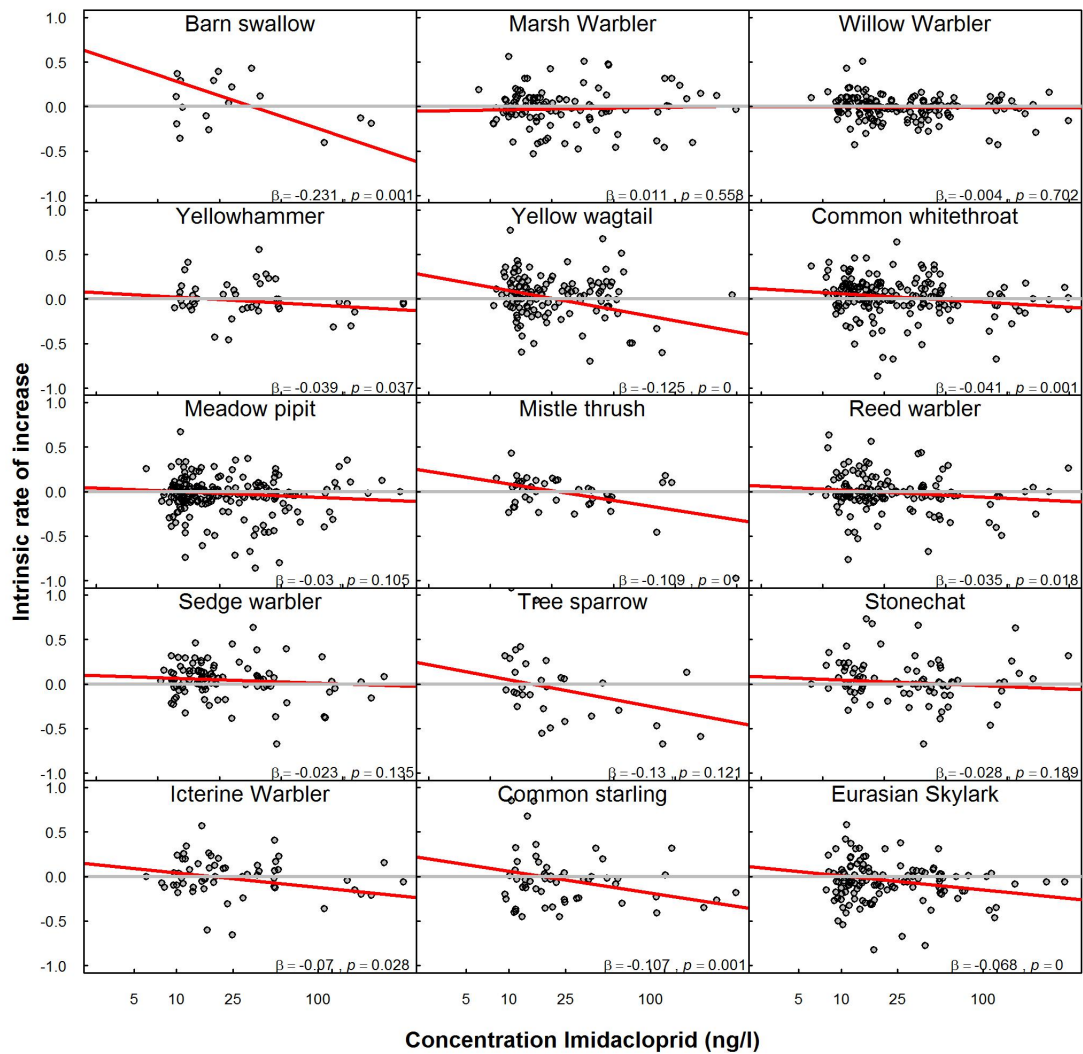


Supplementary Figure A2: Distribution of the 354 bird monitoring plots used in the main analysis.

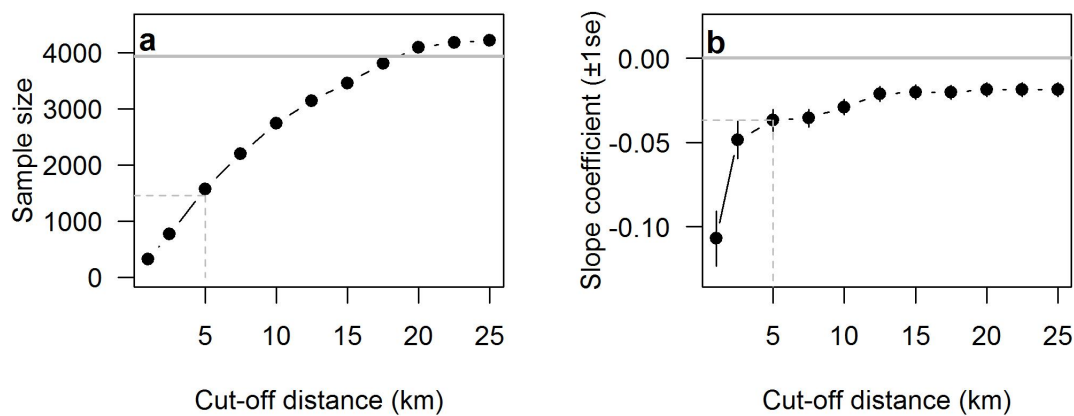


Supplementary Figure A3: Spatial and serial (yearly) autocorrelation of imidacloprid measurements. **a:** Semivariance (dots) and matern variogram model (fitted line) used in the interpolation of the concentrations (nugget=0.1901, sill=1.6989, range=13.2 km). **b:** Serial correlation (between years) of imidacloprid concentrations. Each value gives the number of pairs of measurements at each year-lag that were used to calculate the coefficients. Serial correlations remain invariant with respect to temporal lag, indicating high temporal consistency in local imidacloprid concentrations.

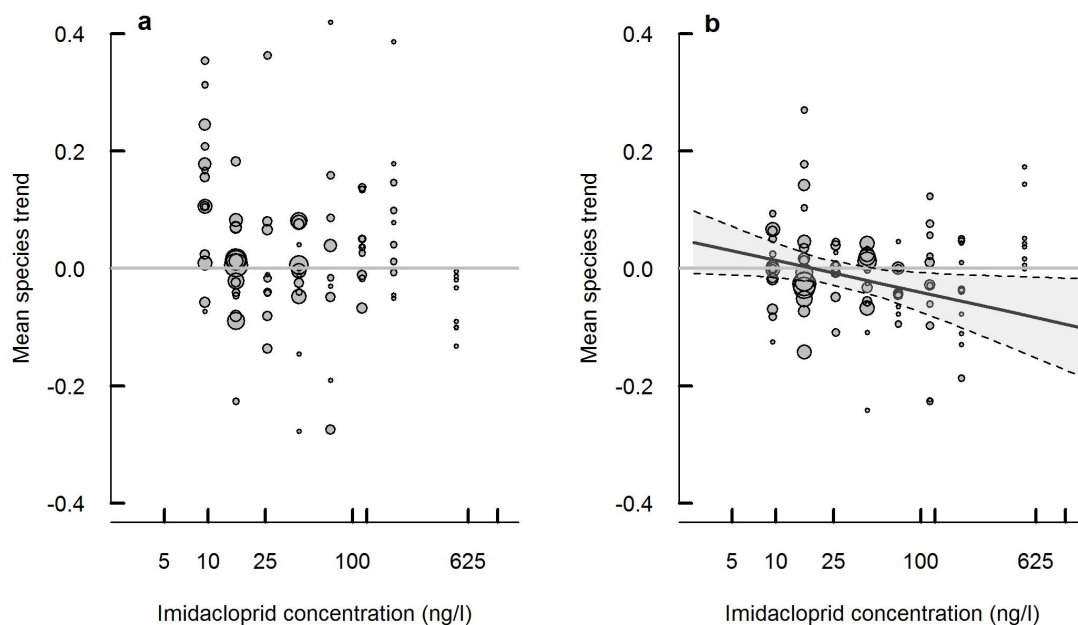




Supplementary Figure A4: Population trends as a function of imidacloprid concentration per individual bird species. The red lines depict the weighted mean trend, also given as slope coefficients ( $\beta$ ), and with corresponding  $P$ -values.



Supplementary Figure A5: Robustness check for the effect of the cut-off value for the distance between bird monitoring plots and water measurement locations (varied between 1 and 25 km). The larger the cut-off distance, the more species-plot annual rates of increase are retained in the analyses subset of the total database of 3947 records (a), but at the cost of increased noise in the response, and a decrease in effect of imidacloprid on the bird trends (b). However, in all cases the effect of imidacloprid was negative and significantly so ( $P < 0.0001$ )



Supplementary Figure A6: Comparison of the relationship of bird species trends in the periods 1984-1995 (a) and 2003-2010 (b) to imidacloprid concentrations in 2003-2009, based on all plots monitored in both time periods. Each point in the scatter plot represents the average intrinsic rate of increase of a species over all plots in the same concentration class. Binning into classes was performed to reduce scatter noise and aid visual interpretation. Actual analyses and the depicted significant regression line were based on raw data. Bird trends in 2003-2010 (after imidacloprid administration) were significantly affected by imidacloprid concentrations ( $t=-2.16$ ,  $df=365$ ,  $P=0.031$ ), but not in the period before imidacloprid administration ( $t=-1.43$ ,  $df=365$ ,  $P=0.15$ ).

## Supplementary Tables

Supplementary Table A1: Species information

| Species   | Foraging habitat   | Migratory behaviour | Trend 1990-2005   |
|---|--------------------|---------------------|-------------------|
| Marsh warbler ( <i>Acrocephalus palustris</i> )     | reed               | long-distance       | stable            |
| Sedge warbler ( <i>Acrocephalus schoenobaenus</i> ) | reed               | long-distance       | strong increase   |
| Reed warbler ( <i>Acrocephalus scirpaceus</i> )     | reed               | long-distance       | stable            |
| Eurasian skylark ( <i>Alauda arvensis</i> )         | farmland/grassland | short-distance      | strong decline    |
| Meadow pipit ( <i>Anthus pratensis</i> )            | grassland          | short-distance      | moderate decline  |
| Yellowhammer ( <i>Emberiza citrinella</i> )         | farmland           | resident            | moderate increase |
| Icterine warbler ( <i>Hippolais icterina</i> )      | gardens/farms      | long-distance       | moderate decline  |
| Barn swallow ( <i>Hirundo rustica</i> )             | farmland/grassland | long-distance       | stable            |
| Yellow wagtail ( <i>Motacilla flava</i> )           | farmland           | long-distance       | moderate decline  |
| Tree sparrow ( <i>Passer montanus</i> )             | farmland           | resident            | stable            |
| Willow warbler ( <i>Phylloscopus trochilus</i> )    | shrubs             | long-distance       | moderate decline  |
| Stonechat ( <i>Saxicola rubicola</i> )              | shrubs             | short-distance      | strong increase   |
| Common starling ( <i>Sturnus vulgaris</i> )         | grassland          | short-distance      | moderate decline  |
| Common whitethroat ( <i>Sylvia communis</i> )       | shrubs             | long-distance       | moderate increase |
| Mistle thrush ( <i>Turdus viscivorus</i> )          | grassland          | short-distance      | moderate decline  |

Supplementary Table A2: Multiple mixed effects regression of population trends (pooled over 15 species,  $n=1926$ ) against log-imidacloprid concentration (ng/l), the area coverage change (difference in proportion of area, see Supplementary Data) of six land use variables related to agricultural intensification, and two variables potentially confounded with imidacloprid concentrations. For each explanatory variable we present the slope coefficient along with the standard error,  $t$ - and  $P$ -values.

|                            | Coefficient(se)             | $t$ -value | $P$ -value |
|----------------------------|-----------------------------|------------|------------|
| Intercept                  | 0.0932(0.0262)              | 3.5500     | 0.0004     |
| Imidacloprid concentration | -0.0294(0.0077)             | -3.8254    | 0.0001     |
| Bulb area                  | 0.0063(0.0032)              | 1.9895     | 0.0468     |
| Urban area                 | -0.2970(0.2293)             | -1.2954    | 0.1954     |
| Fallow land area           | 1.2899(1.1428)              | 1.1287     | 0.2592     |
| Natural area               | -0.1878(0.2173)             | -0.8646    | 0.3874     |
| Nitrogen rates             | $1.15(2.22) \times 10^{-5}$ | 0.5174     | 0.6050     |
| Greenhouse area            | 0.0409(0.1340)              | 0.3050     | 0.7604     |
| Winter cereals area        | 0.0543(0.3950)              | 0.1375     | 0.8906     |
| Maize area                 | -0.0095(0.2062)             | -0.0463    | 0.9631     |



# Appendix B: Supplementary material for Chapter 3

## Supporting Information

### Supplementary Code and Datasets

Supplementary code can be found at <https://doi.org/10.1371/journal.pone.0185809.s003> Supplementary datasets 1 and 2 can be found at <https://doi.org/10.1371/journal.pone.0185809.s004> and <https://doi.org/10.1371/journal.pone.0185809.s005> respectively.

### Malaise trap permissions

According to the German laws and regulations, permissions are necessary in order to perform investigations with malaise traps, at all locations. Permissions for investigations outside as well as within protected areas for the investigations were given by the following authorities (“„Höheren & Unteren Landschaftsbehörden”“). These permits include cover both the entry into protected areas, as well as the trapping of species that have a protected status pursuant to German law (“ „Bundesartenschutzverordnung (BArtSchV)“ )” and “„Bundesnaturschutzgesetz (BNatSchG)”“).

Authorities issuing the permissions for the investigations are listed below (location abbreviations in brackets).

- Struktur und Genehmigungsdirektion Nord (SGD), Rheinland-Pfalz (POM1)
- Landesamt für Umwelt (LfU), Brandenburg, Biologische Station Beeskow (BKL1, GRI1, LAN1)
- Untere Landschaftsbehörde, Kreis Kleve (SCH1)
- Untere Landschaftsbehörde, Kreis Viersen (BRA1-4, RAH1-2)
- Untere Landschaftsbehörde, Kreis Wesel (BIR1, BIS1-10, HUK1, KAN1-2, LOO1, PLI1-2, SLL1, XAN1-2)
- Untere Landschaftsbehörde, Kreis Mettmann (PIM1)
- Untere Landschaftsbehörde, Kreis Düren (SOL1-2)

- Untere Landschaftsbehörde, Stadt D"usseldorf (URD1-2)
- Untere Landschaftsbehörde, Stadt Köln (WAN1)
- Untere Landschaftsbehörde, Stadt Krefeld (BOO1, CAR1, GEO1, NIE1, ORB1-2, SPE1)
- Untere Landschaftsbehörde, Oberbergischer Kreis (LIN1-2)
- Untere Landschaftsbehörde, Rhein Kreis Neuss (SPE2)
- Untere Landschaftsbehörde, Rhein-Sieg-Kreis (WAH1-6, WAN3-4)

### Malaise traps

In this appendix we give more details about the malaise traps, collecting design, and accompanying methods of biomass measurement as designed and applied by the Entomological Society Krefeld. These are also described in German publications [29-31].

The traps used for our research were identically built by the Entomological Society Krefeld itself. Since 1982 the Entomological Society Krefeld has produced malaise traps on the basis of a single cut pattern. This cut pattern is preserved in the archive of the Entomological Society Krefeld and has served as a template for the construction of all traps used in this research. Likewise, the connections of the trap with the bottle in which insects were collected were always constructed in exactly the same way based on reproductions of an template produced in 1982. These self-constructed and identical traps were very similar to the bi-coloured Malaise traps first described by Townes (1972). All aspects of the sampling was therefore standardized: trap construction, size and design (see figures below), colour, netting and stainless steel connections with the collection bottles.

The traps were also applied using a fixed sampling design. Each trap was placed in such a way that there was no shadow on the roof of the trap in order not to influence the sampling. The catch head was aligned to the south by using of a compass to make sure that the entry of the insects into the traps was always from the east and west. At the four corners, wooden poles were placed to adjust the height of the trap and thus the active catch area to the set standard. In all cases, the trap was tightly connected to the ground to ensure that no insects could slip between the ground and the netting.

In summary, the standardization of the sampling design were undertaken with the idea of quantitative analyses of flying insect biomass across years and sites in protected areas.



[!h]

Supplementary Figure B1: **Malaise trap design** with fixed dimension, materials and orientation. Middle height from the ground at the catch head, directed to the south: 190cm. Corner height from ground of the opening on the south side: 110cm. Corner height from ground of the opening on the north side: 90cm. Length of the opening - 190cm. Catch area: 1.89 m<sup>2</sup> west and 1.89 m<sup>2</sup> east: total catch area (opening) 3.78 m<sup>2</sup>.

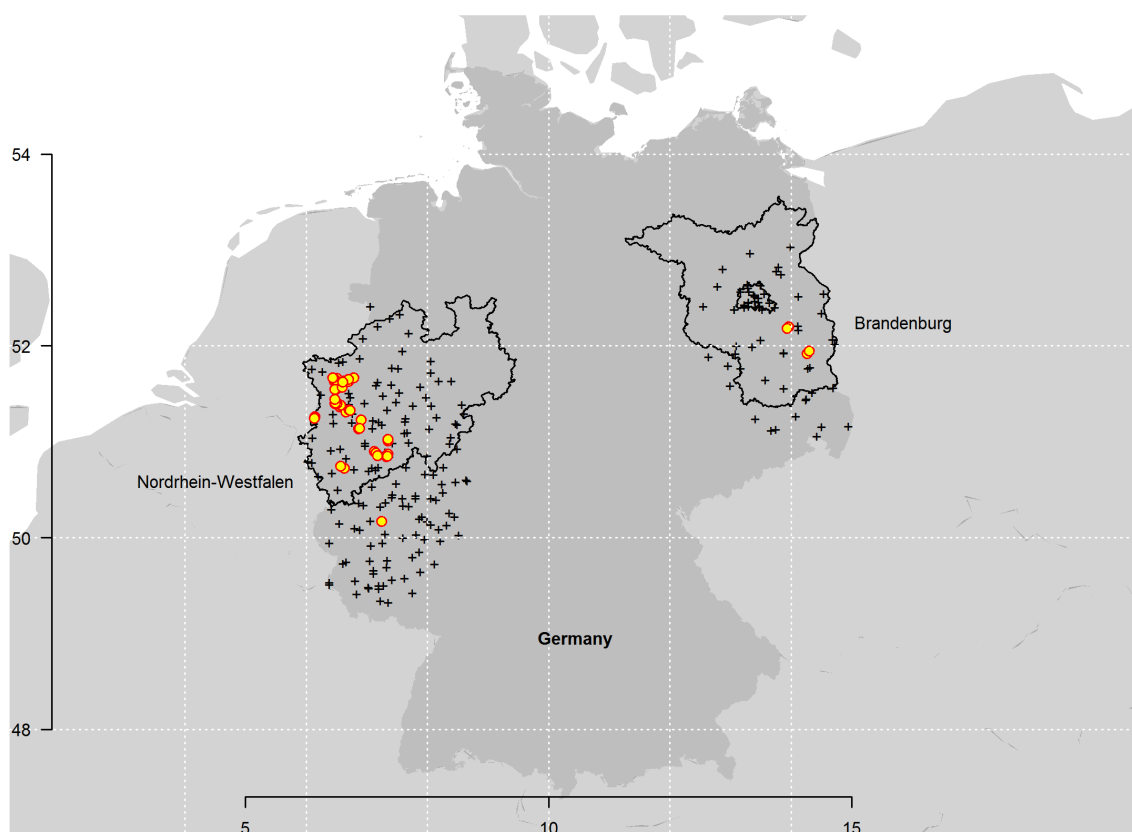
## Supplementary Figures



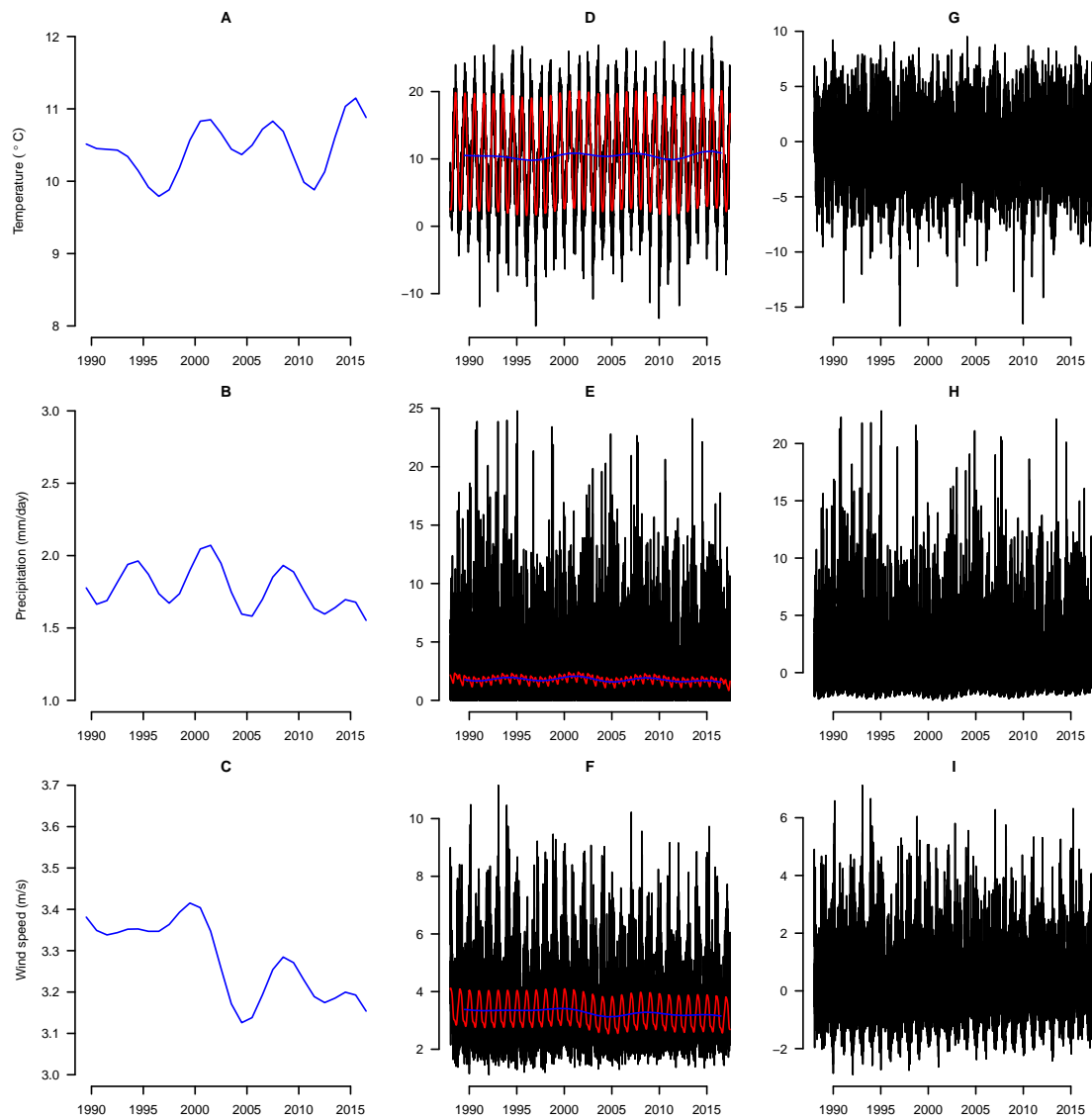


[!h]

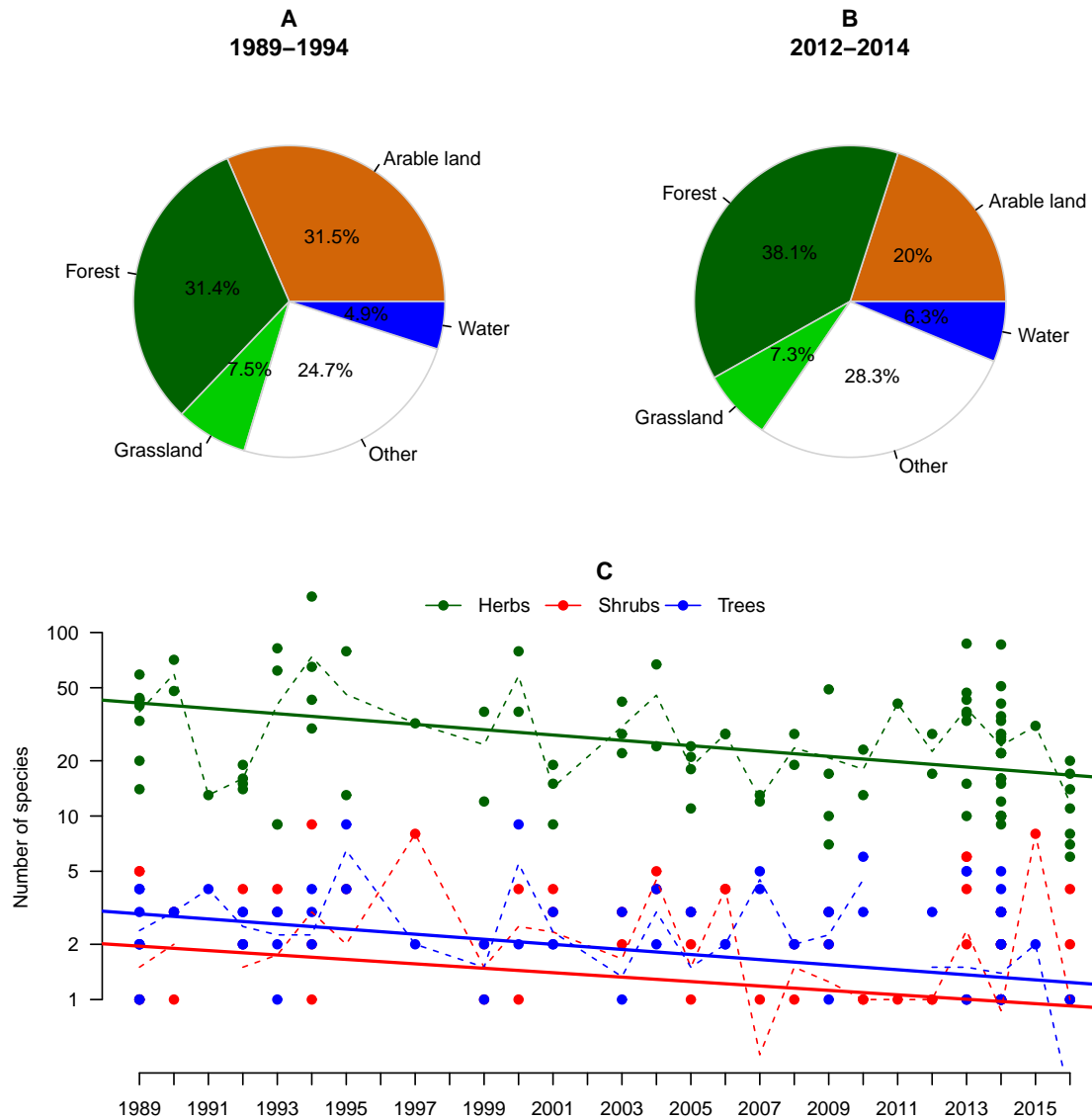
Supplementary Figure B2: **Malaise trap design** with fixed dimension, materials and orientation



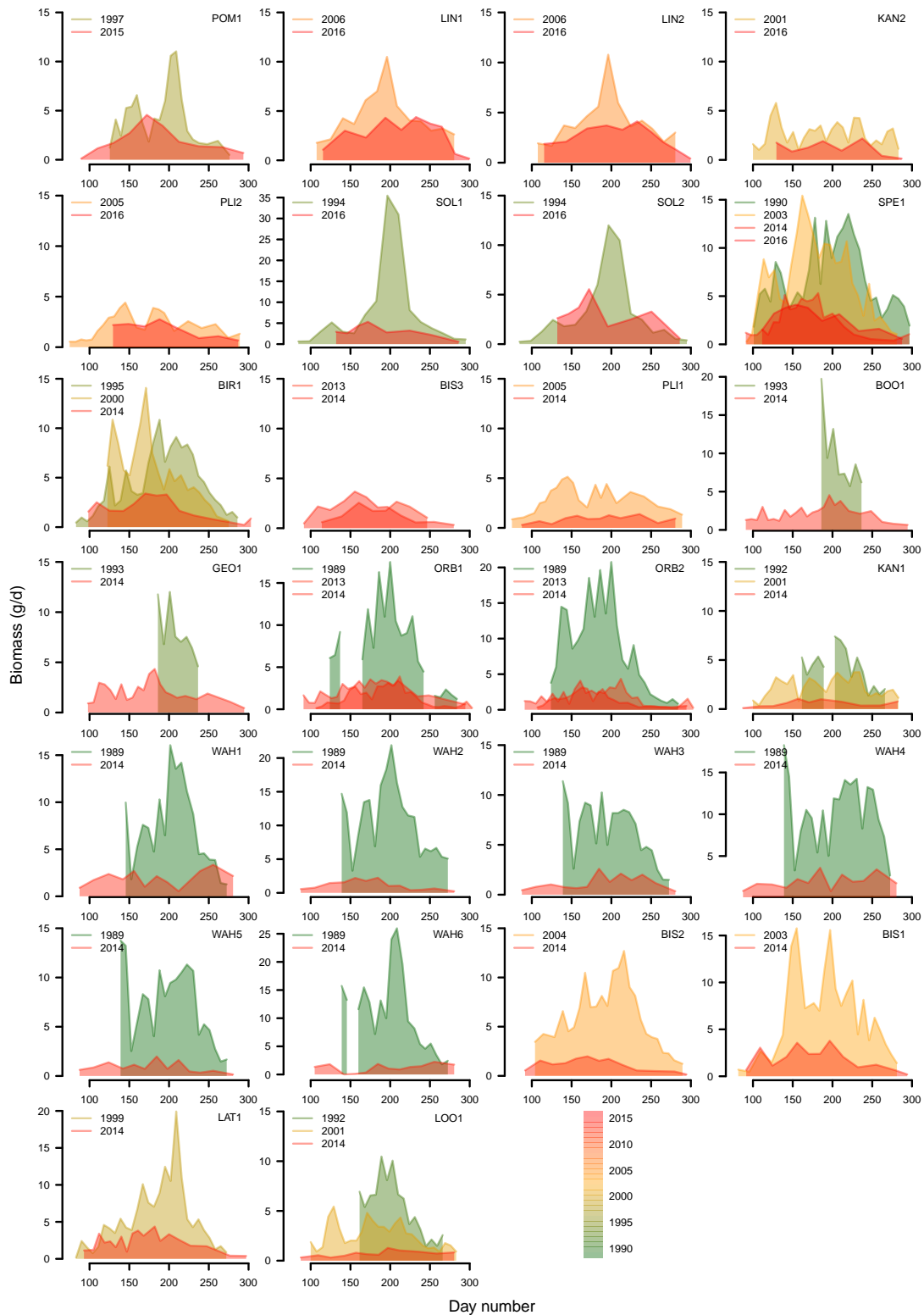
Supplementary Figure B3: **Map of study area.** Insect trap locations (yellow points) in Nordrhein-Westfalen (n=57), Rheinland-Pfalz (n=1) and Brandenburg (n=5), as well as weather stations (crosses) used in the present analysis.



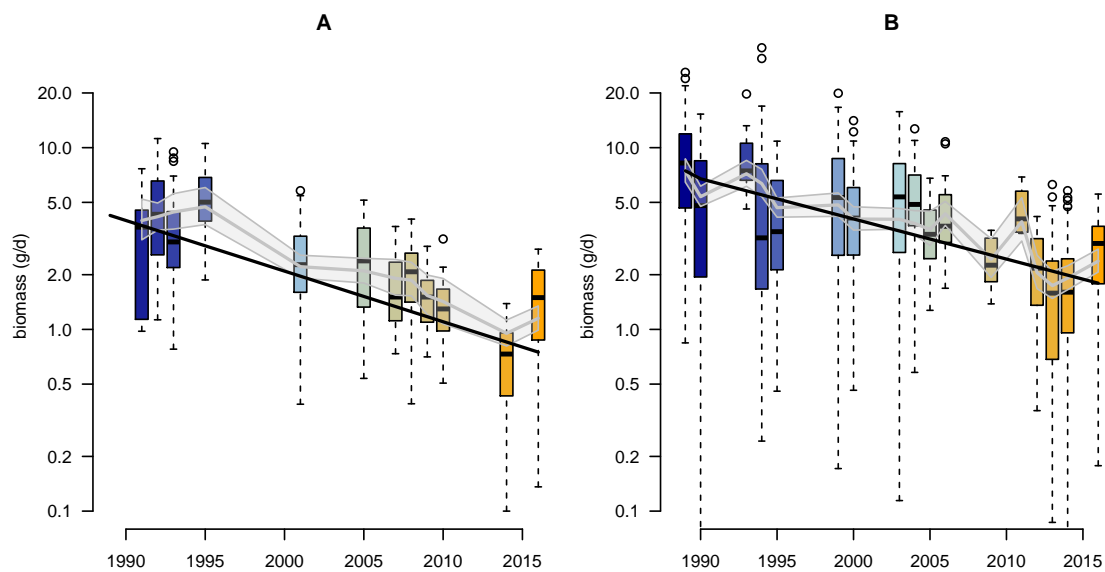
Supplementary Figure B4: **Temporal variation in weather variables.** Annual means (A-C), daily means (D-F), and mean daily residual values (G-I) of temperature, precipitation and wind speed respectively. In all panels, black lines depict data while blue and red lines represent long term and seasonal fitted means of the variables, respectively.



Supplementary Figure B5: **Land use and plant species richness changes.** Mean land use in 1989-1994 (A) and 2012-2014 (B), based on aerial photograph analysis at 63 protected areas show a decrease of arable land and an increase in forested area over the past 25 years. (C) Changes in plants species richness for herbs (black) shrubs (red) and trees (blue). Annual means as well as mean trends are depicted in the corresponding colors. Linear trends are based on generalized linear mixed effects models with a Poisson error distribution and a random intercept effect for location. Note, zero values for tree and shrub species not depicted.



Supplementary Figure B6: **Seasonal profiles of daily biomass across 26 locations.** For each location, different colors represent different years, with time color-coded from green (1989) to red (2016). X-axis represents day number (January 1 = 0).



Supplementary Figure B7: **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 year at trap locations in nutrient-poor heathland, sandy grassland, and dunes (A), and in nutrient-rich grasslands, margins and wasteland (B). Grey lines depict the fitted mean (+95% posterior credible intervals), while the black lines the mean estimated trend. Estimated annual decline amounts to 7.5% (6.6-8.4) for habitat cluster 1, as compared to 5.2% (4.8-5.5) habitat cluster 2. Models fitted independently for each habitat location. Color gradient in all panels range from 1989 (blue) to 2016 (orange).

## Supplementary Tables

Supplementary Table B1: **Posterior parameter estimates of the mixed effects model including weather variables.** For each included variable, the corresponding coefficient posterior mean, standard deviation and 95% credible intervals are given. P-values are calculated empirically based on posterior distributions of coefficients.

| Variable                              | mean   | sd    | 2.50%  | 97.50% | P      |     |
|---------------------------------------|--------|-------|--------|--------|--------|-----|
| Intercept                             | 1.947  | 0.086 | 1.772  | 2.112  | <0.001 | *** |
| $\log(\lambda)$                       | -0.058 | 0.002 | -0.062 | -0.054 | <0.001 | *** |
| Day number                            | -0.127 | 0.029 | -0.185 | -0.069 | <0.001 | *** |
| Day number <sup>2</sup>               | -0.437 | 0.030 | -0.495 | -0.378 | <0.001 | *** |
| Temperature                           | 0.298  | 0.023 | 0.251  | 0.343  | <0.001 | *** |
| Precipitation                         | -0.062 | 0.034 | -0.134 | 0.002  | 0.030  | *   |
| Wind speed                            | 0.005  | 0.026 | -0.046 | 0.057  | 0.418  |     |
| Frost days                            | -0.003 | 0.019 | -0.041 | 0.034  | 0.430  |     |
| Winter Precipitation                  | 0.025  | 0.019 | -0.012 | 0.062  | 0.096  | .   |
| Habitat Cluster 2                     | 0.298  | 0.090 | 0.117  | 0.479  | 0.001  | *** |
| Habitat Cluster 3                     | 0.264  | 0.199 | -0.121 | 0.649  | 0.091  | .   |
| Year $\times$ Day number              | -0.001 | 0.001 | -0.004 | 0.002  | 0.202  |     |
| Year $\times$ Day number <sup>2</sup> | 0.009  | 0.001 | 0.007  | 0.012  | <0.001 | *** |
| $\sigma_{site}$                       | 0.294  | 0.032 | 0.238  | 0.365  |        |     |
| $\nu$                                 | 0.884  | 0.009 | 0.866  | 0.902  |        |     |

Supplementary Table B2: **Posterior parameter estimates of the mixed effects model including land use variables and interactions.** For each included variable, the corresponding coefficient posterior mean, standard deviation and 95% credible intervals are given. P-values are calculated empirically based on posterior distributions of coefficients.

| Variable                       | mean   | sd    | 2.50%  | 97.50% | P      |     |
|--------------------------------|--------|-------|--------|--------|--------|-----|
| Intercept                      | 2.551  | 0.146 | 2.248  | 2.832  | <0.001 | *** |
| Year                           | -0.084 | 0.007 | -0.098 | -0.068 | <0.001 | *** |
| Day number                     | -0.125 | 0.030 | -0.183 | -0.066 | <0.001 | *** |
| Day number <sup>2</sup>        | -0.631 | 0.026 | -0.681 | -0.578 | <0.001 | *** |
| Arable land                    | -0.848 | 0.191 | -1.212 | -0.467 | <0.001 | *** |
| Forest                         | -0.529 | 0.204 | -0.923 | -0.125 | 0.006  | **  |
| Grassland                      | 0.809  | 0.235 | 0.344  | 1.267  | <0.001 | *** |
| Water                          | -0.475 | 0.212 | -0.890 | -0.067 | 0.011  | *   |
| Habitat Cluster 2              | 0.449  | 0.102 | 0.246  | 0.651  | <0.001 | *** |
| Habitat Cluster 3              | 0.415  | 0.212 | -0.005 | 0.838  | 0.026  | *   |
| Year × Day number              | 0.001  | 0.001 | -0.002 | 0.004  | 0.215  |     |
| Year × Day number <sup>2</sup> | 0.011  | 0.001 | 0.009  | 0.014  | <0.001 | *** |
| Year × Arable land             | 0.040  | 0.009 | 0.022  | 0.057  | <0.001 | *** |
| Year × Forest                  | 0.030  | 0.011 | 0.007  | 0.050  | 0.005  | **  |
| Year × Grassland               | -0.062 | 0.014 | -0.090 | -0.033 | <0.001 | *** |
| Year × Water                   | 0.004  | 0.014 | -0.024 | 0.032  | 0.399  |     |
| $\sigma_{site}$                | 0.306  | 0.035 | 0.245  | 0.380  |        |     |
| $\nu$                          | 0.905  | 0.009 | 0.888  | 0.923  |        |     |



Supplementary Table B3: **Posterior parameter estimates of the mixed effects model including habitat variables.** For each included variable, the corresponding coefficient posterior mean, standard deviation and 95% credible intervals are given. P-values are calculated empirically based on posterior distributions of coefficients.

| Variable                       | mean   | sd    | 2.50%  | 97.50% | P      |     |
|--------------------------------|--------|-------|--------|--------|--------|-----|
| Intercept                      | 2.385  | 0.188 | 1.999  | 2.768  | <0.001 | *** |
| Year                           | -0.059 | 0.003 | -0.065 | -0.054 | <0.001 | *** |
| Day number                     | -0.107 | 0.030 | -0.167 | -0.048 | <0.001 | *** |
| Day number <sup>2</sup>        | -0.633 | 0.025 | -0.681 | -0.583 | <0.001 | *** |
| Herb species                   | -0.087 | 0.049 | -0.181 | 0.009  | 0.036  | *   |
| Tree species                   | 0.105  | 0.033 | 0.043  | 0.170  | 0.001  | *** |
| Nitrogen                       | 0.234  | 0.071 | 0.101  | 0.375  | <0.001 | *** |
| pH                             | -0.051 | 0.061 | -0.173 | 0.066  | 0.203  |     |
| Moisture                       | 0.039  | 0.051 | -0.061 | 0.139  | 0.220  |     |
| Light                          | 0.185  | 0.041 | 0.106  | 0.267  | <0.001 | *** |
| Ell. Temperature               | -0.071 | 0.029 | -0.128 | -0.013 | 0.007  | **  |
| Habitat Cluster 2              | 0.350  | 0.159 | 0.036  | 0.654  | 0.014  | *   |
| Habitat Cluster 3              | 0.291  | 0.248 | -0.203 | 0.781  | 0.120  |     |
| Year × Day number              | 0.001  | 0.002 | -0.002 | 0.004  | 0.325  |     |
| Year × Day number <sup>2</sup> | 0.012  | 0.001 | 0.009  | 0.014  | <0.001 | *** |
| $\sigma_{site}$                | 0.315  | 0.036 | 0.251  | 0.395  |        |     |
| $\nu$                          | 0.909  | 0.009 | 0.891  | 0.927  |        |     |

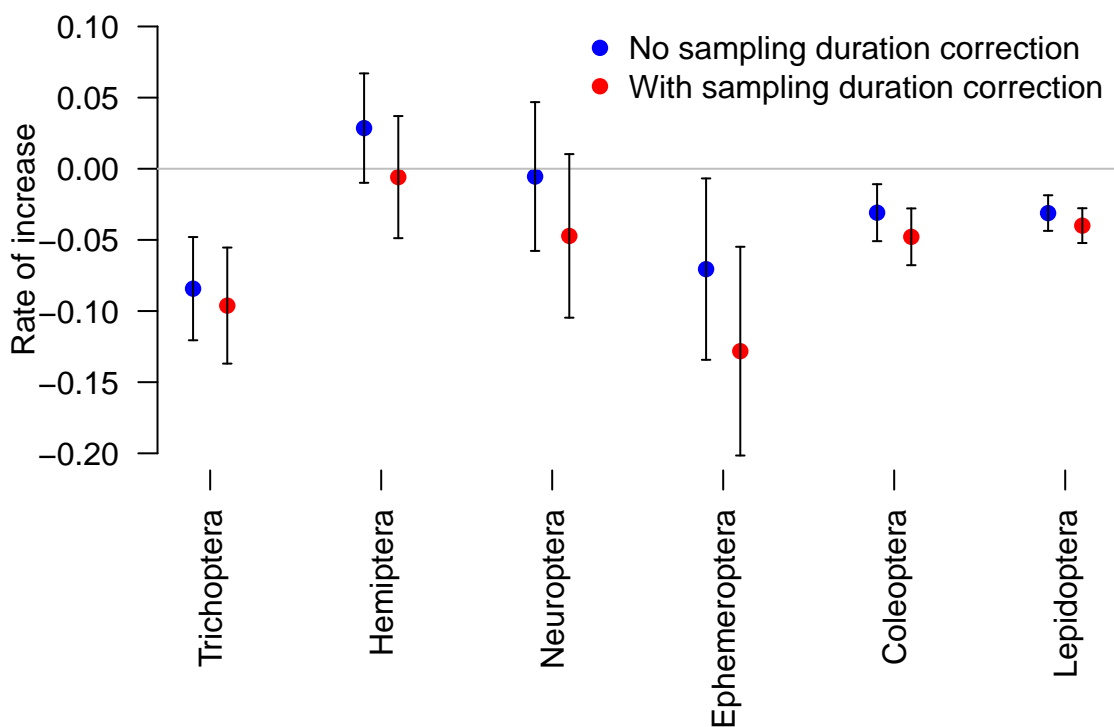
## Appendix C: Supplementary material for Chapter 4

### Supplementary Figures

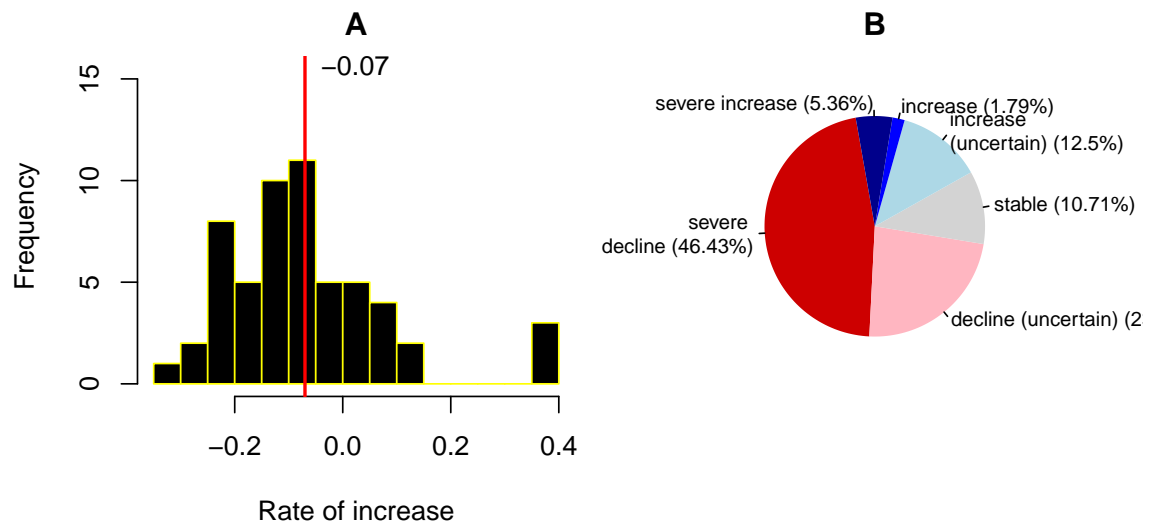
Supplementary Figure C1: At De Kaaistoep site night-active insects (right) were attracted by light in combination with a white sheet (left). Pictures by Paul van Wielink.



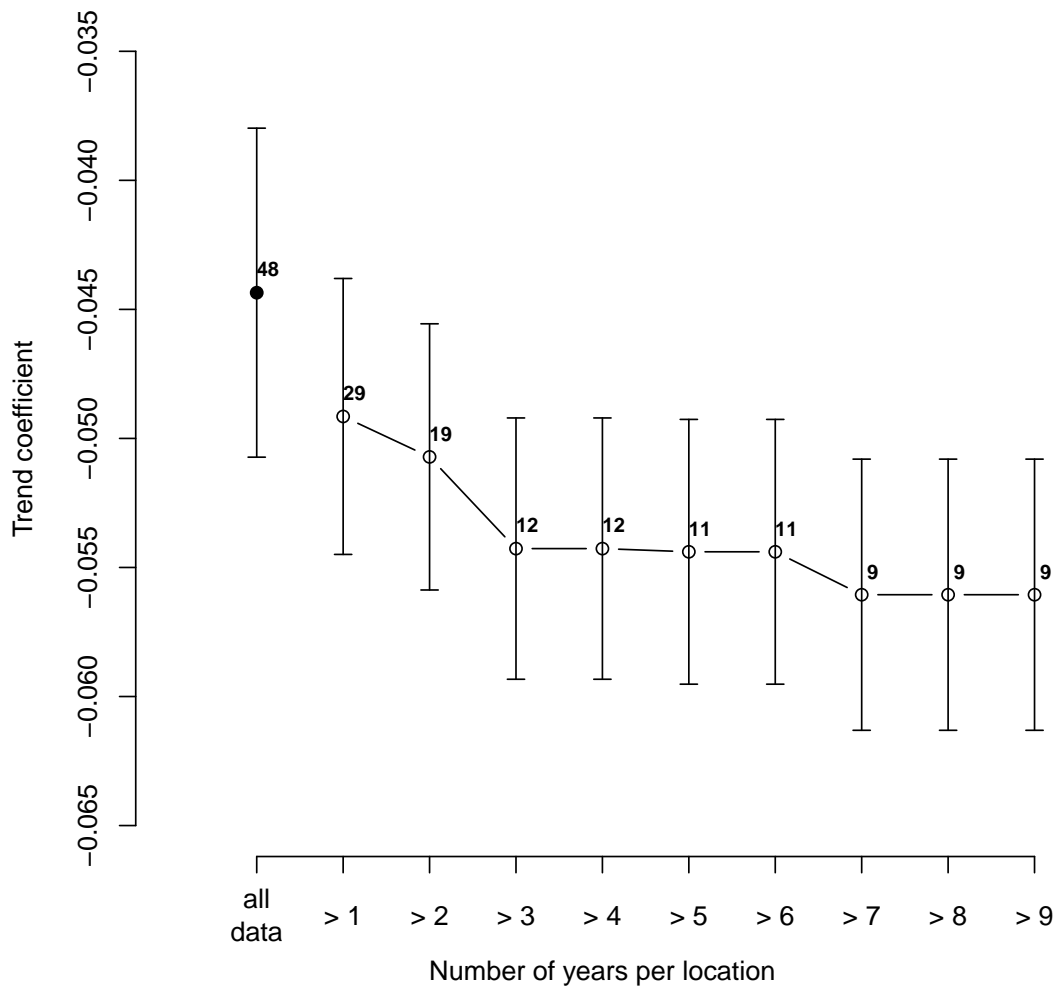
Supplementary Figure C2: One of the pitfall trap locations near Kralo, in the Wijster region, 2017. Picture by Rikjan Vermeulen.



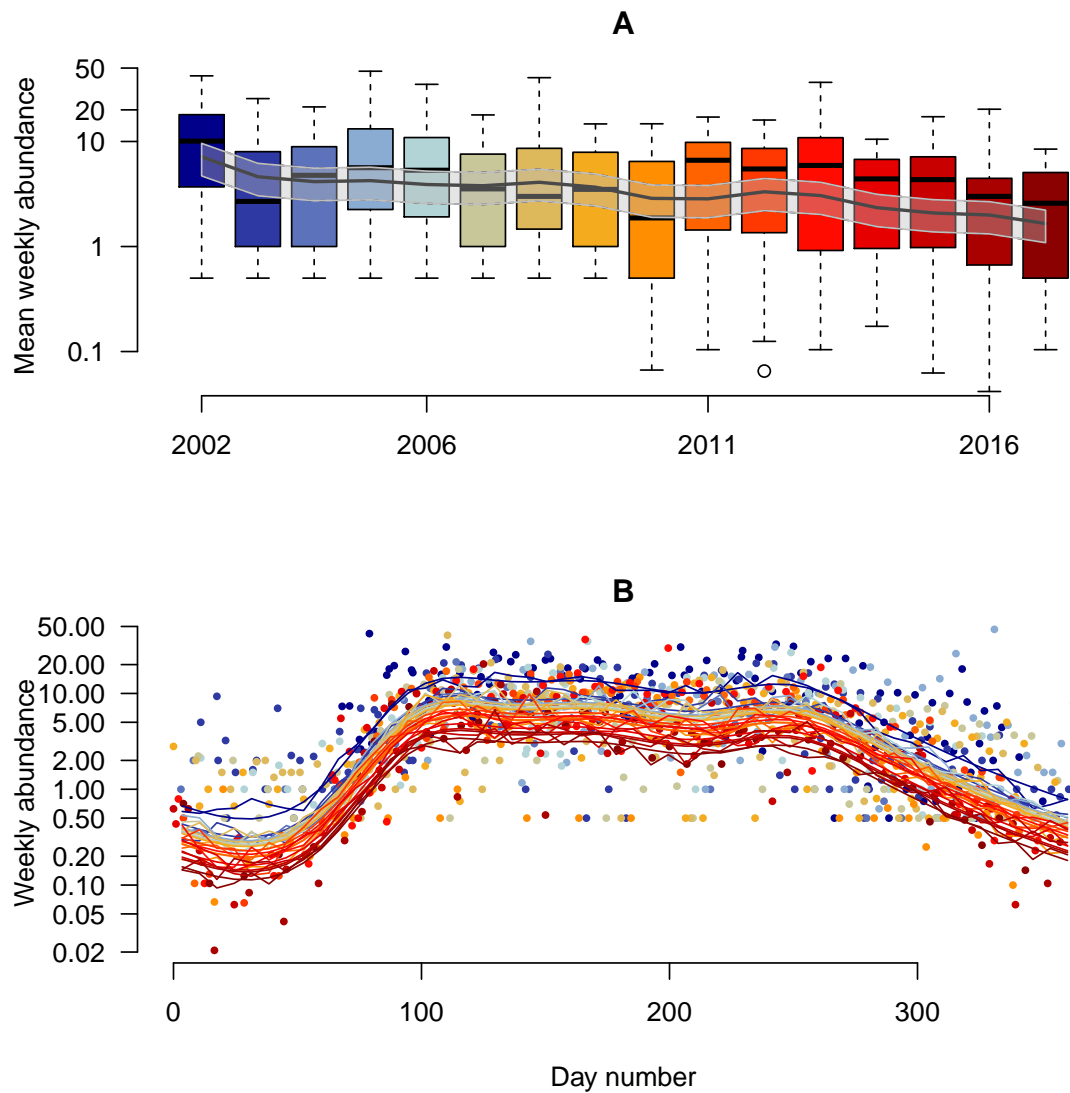
Supplementary Figure C3: Mean annual intrinsic rate of increase ( $\rho$ ) for each insect order based on the data from De Kaaistoep, with and without correction for sampling duration. All estimates are based on the data subset for which information on sampling was available.



Supplementary Figure C4: Histogram (A) and pie diagram (B) for individual species trends (n=56) of ground beetles in De Kaaistoep. See Supplementary Table C4 for the definitions of the trend categories.



Supplementary Figure C5: Annual trend coefficient ( $\pm 1$  standard error) for subsets of the Wijster data. Each point depicts the trend as calculated for all locations that were sampled in more than a particular number of years. Numbers in the graph indicate the number of locations included in the analyses.



Supplementary Figure C6: Mean weekly abundance of ground beetles (Coleoptera: Carabidae) near Wijster over the period 2002-2017. A: Boxplots represent the distribution of the number of individuals (scaled to counts per week) in each year, while the plotted line represent weather-corrected predictions based on model  $G_5$ . The shaded area indicates the 95% confidence levels. B: Seasonal distribution of total numbers of ground beetles (points) along with weather-corrected model predictions for each year. Colors match those in panel A.

## Supplementary Tables

Supplementary Table C1: Model expressions considered for each insect response variable for De Kaaistoep data. Covariates  $t$ ,  $d$  and  $h$  represent year, day of year (i.e. 1 = 1 January), and number of sampling hours respectively, while  $\mathbf{W}$  denotes a design matrix with weather covariates and their squared values.  $\gamma_s$  and  $\gamma_t$  represent smooth terms (thin plate splines) while  $\alpha$  is the intercept,  $\beta_t$  an annual index,  $\beta_w$  weather coefficients,  $\beta_h$  the sampling duration coefficient, and  $\rho$  the annual log-linear trend coefficient.

| Model | Expression  | Description   |
|-------|---|---|
| $M_0$ | $\alpha + \gamma_s(d) + \beta_t(t) + \beta_h h + \beta_{h2} h^2$                        | seasonal trend, discrete annual index, sampling duration                    |
| $M_1$ | $\alpha + \gamma_s(d) + \rho \times t + \beta_h h + \beta_{h2} h^2$                     | seasonal trend, linear annual trend, sampling duration                      |
| $M_2$ | $\alpha + \gamma_s(d) + \gamma_t(t) + \beta_h h + \beta_{h2} h^2$                       | seasonal trend, non-linear annual trend, sampling duration                  |
| $M_3$ | $\alpha + \gamma_s(d) + \mathbf{W}\beta_w + \beta_t(t) + \beta_h h + \beta_{h2} h^2$    | seasonal trend, discrete annual index, weather effects, sampling duration   |
| $M_4$ | $\alpha + \gamma_s(d) + \mathbf{W}\beta_w + \rho \times t + \beta_h h + \beta_{h2} h^2$ | seasonal trend, linear annual trend, weather effects, sampling duration     |
| $M_5$ | $\alpha + \gamma_s(d) + \mathbf{W}\beta_w + \gamma_t(t) + \beta_h h + \beta_{h2} h^2$   | seasonal trend, non-linear annual trend, weather effects, sampling duration |

Supplementary Table C2: Model expressions considered for each ground beetle species in the Wijster dataset. Covariate  $t$  represents year, while  $\mathbf{W}$  denotes a design matrix with weather covariates and their squared values.  $\gamma_t$  represents a smooth term (thin plate splines), while  $\alpha$  is the intercept,  $\beta_t$  an annual index,  $\beta_w$  weather coefficients,  $b_i$  random location effect, and  $\rho$  the annual log-linear trend coefficient.

| Model | Expression   | Description  |
|-------|--|--|
| $A_0$ | $\alpha + \beta_t(t) + b_i$                        | discrete annual index, random location effect                    |
| $A_1$ | $\alpha + \rho \times t + b_i$                     | linear annual trend, random location effect                      |
| $A_2$ | $\alpha + \gamma_t(t) + b_i$                       | non-linear annual trend, random location effect                  |
| $A_3$ | $\alpha + \beta_t(t) + \mathbf{W}\beta_w + b_i$    | discrete annual index, random location effect, weather effects   |
| $A_4$ | $\alpha + \rho \times t + \mathbf{W}\beta_w + b_i$ | linear annual trend, random location effect, weather effects     |
| $A_5$ | $\alpha + \gamma_t(t) + \mathbf{W}\beta_w + b_i$   | non-linear annual trend, random location effect, weather effects |

Supplementary Table C3: Model expressions considered for weekly data on ground beetles in the Wijster dataset. Covariates  $t$ ,  $d$  and  $s$  represent year, day of year (i.e. 1 = 1 January), and trap, while  $\mathbf{W}$  denotes a design matrix with weather covariates.  $\gamma_s$  and  $\gamma_t$  represent smooth terms (cubic cyclic and thin plate splines, respectively) while  $\alpha$  is the intercept,  $\varepsilon_s$  a random trap effect,  $\beta_w$  weather coefficients, and  $\rho$  the annual log-linear trend coefficient.

| Model | Expression   | Description   |
|-------|--|---|
| $G_0$ | $\alpha + \gamma_s(d) + \beta_t(t) + \varepsilon_s$                        | seasonal trend, discrete annual index, trap effect                    |
| $G_1$ | $\alpha + \gamma_s(d) + \rho \times t + \varepsilon_s$                     | seasonal trend, linear annual trend, trap effect                      |
| $G_2$ | $\alpha + \gamma_s(d) + \gamma_t(t) + \varepsilon_s$                       | seasonal trend, non-linear annual trend, trap effect                  |
| $G_3$ | $\alpha + \gamma_s(d) + \mathbf{W}\beta_w + \varepsilon_s$                 | seasonal trend, discrete annual index, weather effects, trap effect   |
| $G_4$ | $\alpha + \gamma_s(d) + \mathbf{W}\beta_w + \rho \times t + \varepsilon_s$ | seasonal trend, linear annual trend, weather effects, trap effect     |
| $G_5$ | $\alpha + \gamma_s(d) + \mathbf{W}\beta_w + \gamma_t(t) + \varepsilon_s$   | seasonal trend, non-linear annual trend, weather effects, trap effect |

Supplementary Table C4: Trend classification. For a given estimated trend coefficient (intrinsic rate of increase:  $\rho$ ) and significance level, the following classification was applied in order to categorize trends of species.

| Annual log-linear trend coefficient | $p$ -value | Trend classification |
|-------------------------------------|------------|----------------------|
| $\rho < -0.05$                      | $p < 0.05$ | severe decline       |
| $-0.05 < \rho < -0.025$             | $p < 0.05$ | decline              |
| $\rho < -0.025$                     | $p > 0.05$ | decline (uncertain)  |
| $-0.025 < \rho < 0.025$             | -          | stable               |
| $\rho > 0.025$                      | $p > 0.05$ | increase (uncertain) |
| $0.025 > \rho > 0.05$               | $p < 0.05$ | increase             |
| $\rho > 0.05$                       | $p < 0.05$ | severe increase      |



Supplementary Table C5: AIC values of models fitted per insect order for De Kaaistoep data. For model formulations see Supplementary Table C2. Lowest AIC value per insect order (i.e. per row) is given in bold.

| Insect order         | $M_0$   | $M_1$   | $M_2$   | $M_3$          | $M_4$          | $M_5$          |
|----------------------|---------|---------|---------|----------------|----------------|----------------|
| <i>Trichoptera</i>   | 2399.75 | 2409.74 | 2410.98 | <b>2345.17</b> | 2360.18        | 2360.21        |
| <i>Hemiptera</i>     | 2731.27 | 2729.32 | 2731.19 | 2592.28        | <b>2590.72</b> | 2591.73        |
| <i>Neuroptera</i>    | 1028.71 | 1048.14 | 1026.04 | <b>1006.95</b> | 1022.93        | 1009.11        |
| <i>Ephemeroptera</i> | 1532.82 | 1527.96 | 1527.99 | 1531.85        | <b>1524.73</b> | 1524.73        |
| <i>Coleoptera</i>    | 7335.93 | 7347.05 | 7347.28 | 7035.64        | 7032.72        | <b>7032.38</b> |
| <i>Lepidoptera</i>   | 5325.19 | 5348.06 | 5347.82 | <b>5274.71</b> | 5294.32        | 5294.37        |

Supplementary Table C6: Model coefficients (and standard errors) for model  $M_4$  for each of the insect orders at De Kaaistoep. Significant effects at the 5% level are given in bold.

|                            | Trichoptera              | Hemiptera                | Neuroptera              | Ephemeroptera            | Coleoptera               | Lepidoptera              |
|----------------------------|--------------------------|--------------------------|-------------------------|--------------------------|--------------------------|--------------------------|
| Annual trend               | <b>-0.096</b><br>(0.021) | -0.006<br>(0.022)        | -0.047<br>(0.029)       | <b>-0.128</b><br>(0.037) | <b>-0.048</b><br>(0.01)  | <b>-0.04</b><br>(0.006)  |
| Duration                   | -0.457<br>(0.637)        | -0.054<br>(0.608)        | 1.32<br>(0.876)         | 2.454<br>(1.307)         | <b>1.228</b><br>(0.286)  | <b>0.39</b><br>(0.164)   |
| Duration <sup>2</sup>      | 0.087<br>(0.088)         | 0.061<br>(0.084)         | -0.1<br>(0.117)         | -0.251<br>(0.181)        | <b>-0.122</b><br>(0.042) | -0.022<br>(0.024)        |
| Temperature                | <b>4.894</b><br>(0.769)  | <b>6.579</b><br>(0.763)  | 0.841<br>(0.925)        | <b>4.157</b><br>(1.406)  | <b>3.922</b><br>(0.398)  | <b>1.226</b><br>(0.245)  |
| Moisture                   | 0.41<br>(0.762)          | -0.309<br>(0.782)        | <b>2.37</b><br>(1.124)  | <b>3.541</b><br>(1.339)  | <b>1.169</b><br>(0.517)  | 0.142<br>(0.303)         |
| Precipitation              | 0.055<br>(0.188)         | 0.147<br>(0.189)         | 0.349<br>(0.302)        | 0.141<br>(0.33)          | <b>-0.218</b><br>(0.096) | -0.048<br>(0.053)        |
| Temperature <sup>2</sup>   | <b>-3.914</b><br>(0.716) | <b>-4.747</b><br>(0.712) | -0.222<br>(0.859)       | <b>-4.011</b><br>(1.307) | <b>-2.396</b><br>(0.379) | <b>-0.773</b><br>(0.222) |
| Moisture <sup>2</sup>      | -0.436<br>(0.768)        | 0.465<br>(0.79)          | <b>-2.67</b><br>(1.144) | <b>-3.763</b><br>(1.352) | <b>-1.142</b><br>(0.52)  | -0.055<br>(0.312)        |
| Precipitation <sup>2</sup> | -0.138<br>(0.186)        | -0.169<br>(0.181)        | -0.596<br>(0.364)       | -0.113<br>(0.324)        | 0.089<br>(0.09)          | 0.031<br>(0.043)         |

Supplementary Table C7: Degrees of freedom (d.f.), AIC and deviance of the six models (see Supplementary Table C3) fitted to the weekly pitfall trap data on ground beetles in nature reserves near Wijster over the period 2002-2017.

|       | d.f.  | AIC      | Deviance |
|-------|-------|----------|----------|
| $G_0$ | 52.84 | 75917.35 | 15200.13 |
| $G_1$ | 38.72 | 76126.62 | 15215.45 |
| $G_2$ | 46.71 | 75952.16 | 15207.97 |
| $G_3$ | 54.90 | 75519.21 | 15199.01 |
| $G_4$ | 40.78 | 75736.69 | 15191.08 |
| $G_5$ | 48.80 | 75550.79 | 15199.82 |

Supplementary Table C8: Single-term deletions from the global model of trends of Macro-moths in De Kaaistoep. For each of the remaining explanatory variable, the degrees of freedom,  $F$ - and  $p$ -values are given.

| Model term             | d.f | \$F\$ | \$p\$ |
|------------------------|-----|-------|-------|
| Intercept              | 1   | 55.34 | 0.00  |
| Voltinism              | 4   | 0.44  | 0.78  |
| Winter strategy        | 3   | 2.30  | 0.08  |
| Host plant type        | 5   | 2.04  | 0.08  |
| Host plant specificity | 2   | 0.44  | 0.65  |
| Rarity                 | 4   | 2.39  | 0.05  |
| Weight                 | 1   | 0.25  | 0.62  |

Supplementary Table C9: Most parsimonious generalized least-squares model of trends of Macro-moths in De Kaaistoep. Stepwise model selection was based on AIC values. Plant type was the only explanatory variable retained in this model. The intercept represents the factor level 'grass'. For each model coefficient we give the estimated coefficient, standard error,  $t$ -values and  $p$ -values. Additionally, we present the estimate of the variance parameter ( $\phi$ ) relating the residual variance to the log of the mean abundance of each species.

| Model coefficient | Estimate | s.e.  | $t$    | $p$   |
|-------------------|----------|-------|--------|-------|
| intercept         | -0.063   | 0.013 | -4.835 | 0.000 |
| herb              | 0.007    | 0.017 | 0.423  | 0.673 |
| tree/shrub        | 0.049    | 0.018 | 2.761  | 0.006 |
| tree              | 0.035    | 0.016 | 2.182  | 0.030 |
| diverse           | 0.020    | 0.018 | 1.113  | 0.267 |
| other             | 0.058    | 0.022 | 2.590  | 0.010 |
| $\phi$            | -0.343   |       |        |       |

Supplementary Table C10: Single-term deletions of a model for a subset of the trends of Macro-moths in De Kaaistoep, given Ellenberg values for larval-host-plant. For each of the remaining explanatory variabe, the degrees of freedom,  $F$ - and  $p$ -values are given.

| Model term    | d.f | $F$   | $p$   |
|---------------|-----|-------|-------|
| Nitrogen      | 1   | 0.439 | 0.509 |
| Light         | 1   | 0.036 | 0.850 |
| Temperature   | 1   | 2.840 | 0.094 |
| Humidity      | 1   | 0.747 | 0.389 |
| pH            | 1   | 3.882 | 0.051 |
| Continetality | 1   | 0.684 | 0.410 |

Supplementary Table C11: Single-term deletions from the global model of trends of ground beetle species near Wijster. For each of the remaining explanatory variabe, the degrees of freedom,  $F$ - and  $p$ -values are given.

| Model term         | d.f | $F$    | $p$   |
|--------------------|-----|--------|-------|
| Intercept          | 1   | 47.454 | 0.000 |
| Distribution       | 3   | 6.025  | 0.001 |
| Specialization     | 3   | 2.606  | 0.056 |
| Flight ability     | 3   | 2.276  | 0.084 |
| Wintering strategy | 2   | 1.074  | 0.346 |
| log(weight)        | 1   | 5.608  | 0.020 |
| Turin. class       | 3   | 1.973  | 0.123 |

Supplementary Table C12: Most parsimonious generalized least-squares model of ground beetle trends near Wijster. For each model coefficient we present the estimated coefficient, standard error, *t*-values and *p*-values. Please note that the first level of each factor is discounted in the intercept: this applies to the Turin class 'hydrophyllous', eurytopy level 'stenotopic' and distribution level 'marginal'. The final coefficient ( $\phi$ ) relates the residual variance to the log of the mean abundance of each species.

| Parameter          | Level      | Estimate | se    | <i>t</i> | <i>p</i> |
|--------------------|------------|----------|-------|----------|----------|
| Intercept          |            | -0.524   | 0.115 | -4.543   | 0.000    |
| Distribution       | sub marg.  | 0.426    | 0.117 | 3.639    | 0.000    |
|                    | sub centr. | 0.434    | 0.117 | 3.694    | 0.000    |
|                    | centr.     | 0.418    | 0.118 | 3.533    | 0.001    |
| Specialization     | less sten. | 0.055    | 0.037 | 1.472    | 0.144    |
|                    | eury.      | 0.048    | 0.039 | 1.223    | 0.224    |
|                    | very eury. | 0.020    | 0.040 | 0.493    | 0.623    |
| log(weight)        |            | 0.016    | 0.007 | 2.266    | 0.026    |
| Turin. class       | no pref.   | -0.010   | 0.026 | -0.376   | 0.708    |
|                    | Forest     | 0.027    | 0.042 | 0.648    | 0.519    |
|                    | xeroph.    | -0.058   | 0.025 | -2.308   | 0.023    |
| Variance parameter | $\phi$     | -0.217   |       |          |          |



# Appendix D: Supplementary material for Chapter 5

## Supplementary material

### Supplementary Methods

If detectability of individual species is invariant during the season, i.e. they are equally likely to be trapped in each of the pots, then the distribution of number of species in each pot could be approximated in a straightforward manner by a sampling-without-replacement process, conditional on the accumulated community data. However, hoverfly species are not likely to be active during the entire season, leading to non uniform detectability during the season. Formally, the number of species expected to be trapped in a single pot ( $\hat{s}$ ) will depend on the relative abundance of each species ( $N_i$ ), the total abundance in the pot ( $N_j$ ) and total species richness  $S$ , according to

$$\hat{s}(N_j, S) = \sum_i^S \left( 1 - \frac{\binom{N-N_i}{N_j}}{\binom{N}{N_j}} \right)$$

(Hurlbert, 1971) where  $N = \sum N_j = \sum N_i$ .

In equation 5.11 we introduced a correction factor  $c$ , that measures the average availability of species during the season. We used the following approach to obtain an estimate of  $c$ .

First we produced average daily total abundance per pot  $j$  (abundance per pot divided by exposure length) which we denote as  $\hat{n}_j$ . We then calculated the expected number of species given total richness ( $S$ ), total abundance ( $N$ ) and relative species abundance ( $N_i$ ). Additionally, and for each pot, we calculated the expected number of species per day conditional on the number of species seen in each pot ( $S_j$ ).

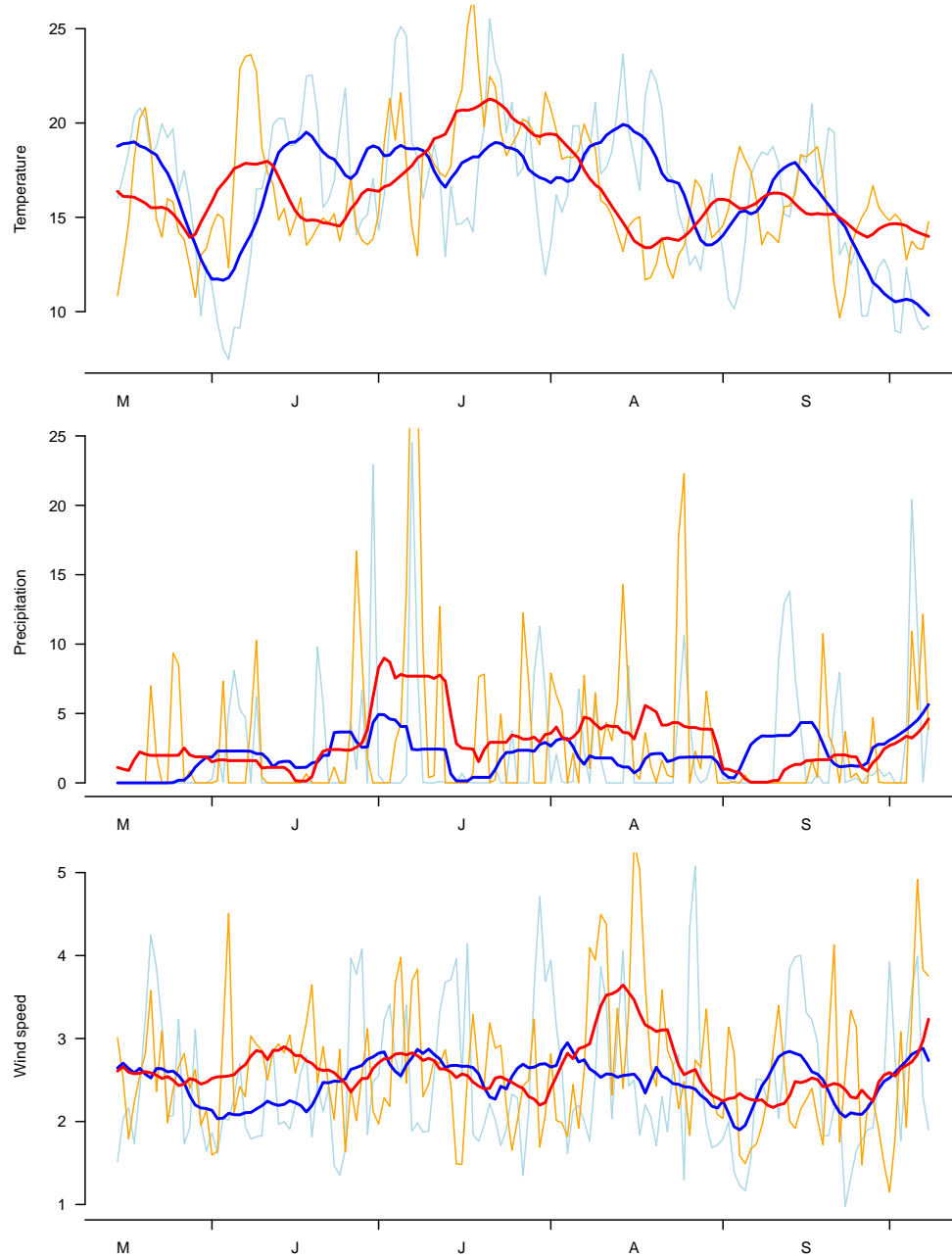
$$\hat{s}_j^{(2)}(\hat{n}_j, S_j) = \sum_i^{S_j} \left( 1 - \frac{\binom{N-N_i}{\hat{n}_j}}{\binom{N}{\hat{n}_j}} \right)$$

The relationship between  $\hat{s}_j^{(1)}(\hat{n}_j, S)$  and  $\hat{s}_j^{(2)}(\hat{n}_j, S_j)$  is linear, with zero intercept and slope  $0 < c \leq 1$ , because typically  $S_j \leq S$ . The coefficient  $c$  is hence obtained as:

$$c = \frac{\hat{s}_j^{(2)}(\hat{n}_j, S_j)}{\hat{s}_j^{(2)}(\hat{n}_j, S)}$$

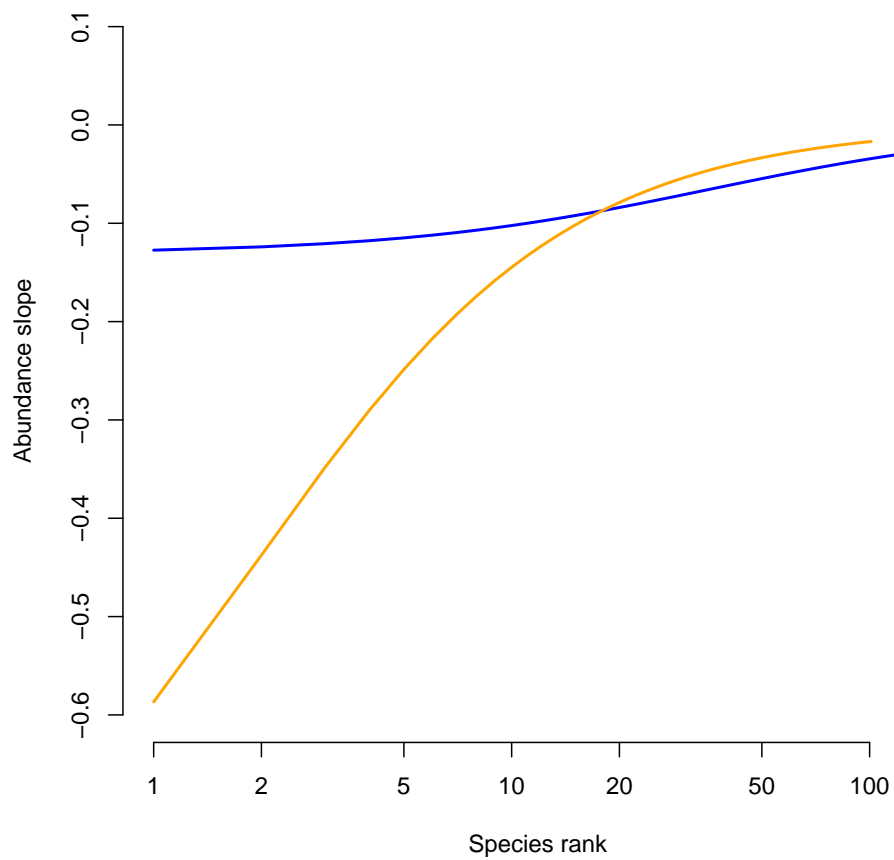
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## Supplementary Figures

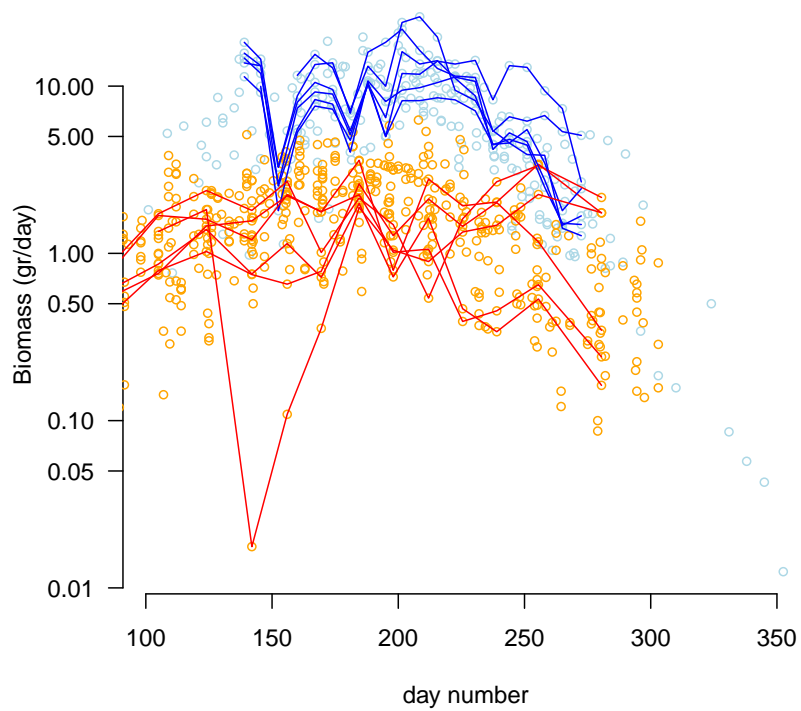


Supplementary Figure D1: Climatic variables in 1989 (light blue) and 2014 (orange) for temperature (in  $C^{\circ}$ ), precipitation (mm/day) and wind speed (m/s). Thick red and blue lines represent the 2-week moving average.

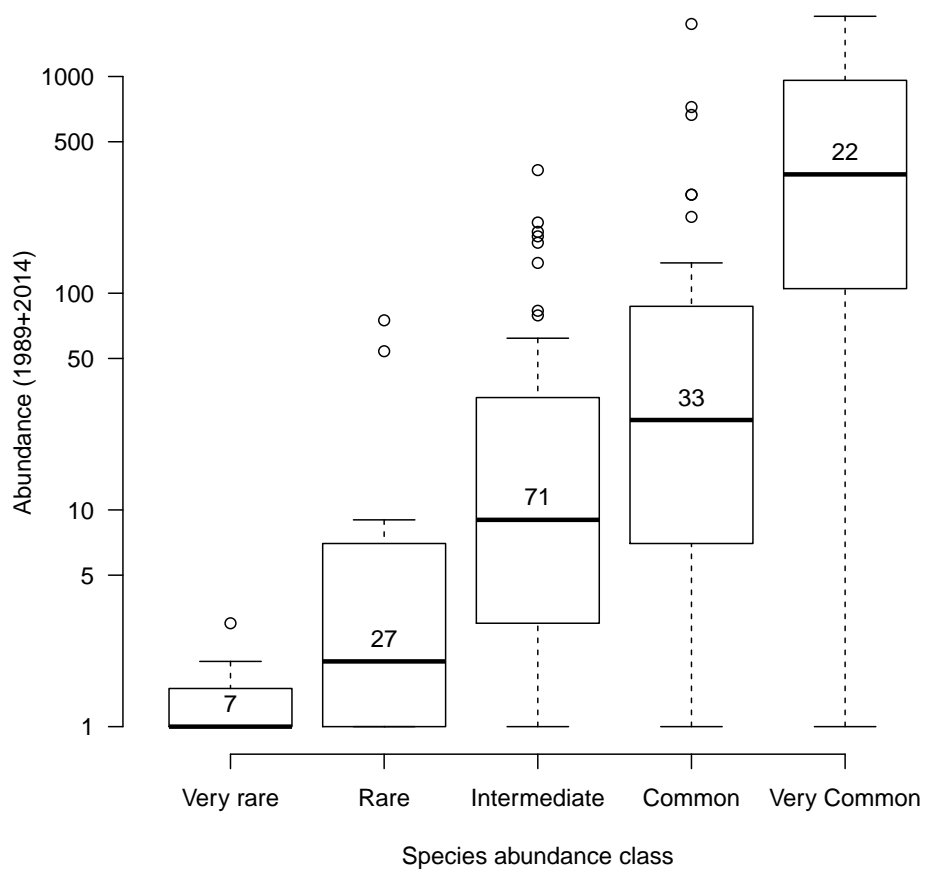




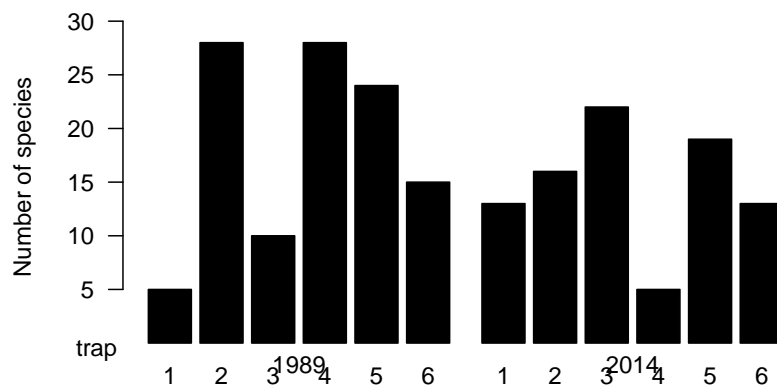
Supplementary Figure D2: Slope of the rank-abundance curve for 1989 (blue) and 2014 (orange) against species rank.



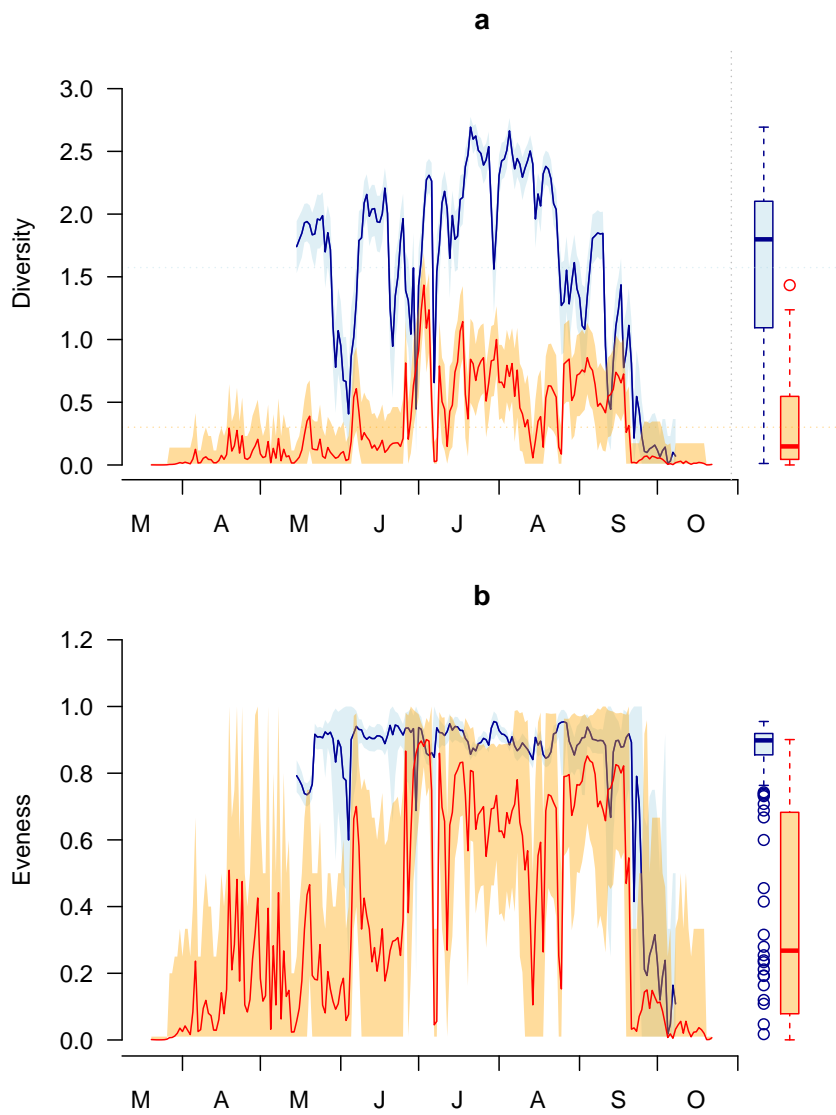
Supplementary Figure D3: Temporal distribution of biomass (in gram per day) of total flying insects for all pots in the period 1989-1992 (light blue dots) and period 2012-2015 (orange dots). Blue and red lines depict the seasonal biomass distribution for the six Wahnbachthal traps examined in 1989 and 2014



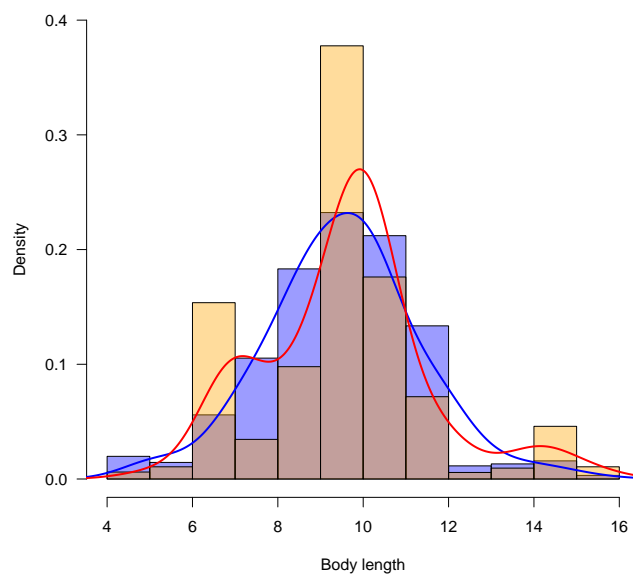
Supplementary Figure D4: Observed abundance (sum of 1998 and 2014 by species) versus abundance class of species in Germany as defined in Ssymank *et al.* (2011). Numbers inside boxplots represent the number of species in that class



Supplementary Figure D5: Observed number of plant species (in the herb layer) in each year and by trap



Supplementary Figure D6: Seasonal Shannon's diversity index (a:  $H'$ ) and evenness (b:  $e$ ) for 1989 (blue) and 2014 (red) as calculated by our model



Supplementary Figure D7: Distribution of body length weighted by specie's numbers for 1989 (blue) and 2014 (red)

Supplementary Table D1: Parameter estimates form posterior distribution for daily total hoverfly abundance. *d*: climatic parameters. *c*: seasonal (quadratic effect) parameters, *b*: trap effects, and  $\log(\lambda)$ : the log-rate of decline from 1989 to 2014.

|                       | mean   | sd    | 2.5%   | 97.5%  | $\hat{R}$ |
|-----------------------|--------|-------|--------|--------|-----------|
| Intercept             | 2.477  | 0.027 | 2.424  | 2.529  | 1.002     |
| $\log(\lambda)$       | -1.756 | 0.028 | -1.808 | -1.697 | 1.001     |
| <i>c</i> <sub>1</sub> | 0.090  | 0.014 | 0.063  | 0.116  | 1.001     |
| <i>c</i> <sub>2</sub> | -0.480 | 0.019 | -0.516 | -0.443 | 1.002     |
| <i>c</i> <sub>3</sub> | 0.476  | 0.033 | 0.412  | 0.541  | 1.001     |
| <i>c</i> <sub>4</sub> | -0.614 | 0.035 | -0.683 | -0.548 | 1.001     |
| <i>d</i> <sub>1</sub> | 0.590  | 0.013 | 0.564  | 0.615  | 1.001     |
| <i>d</i> <sub>2</sub> | -0.367 | 0.032 | -0.432 | -0.310 | 1.001     |
| <i>d</i> <sub>3</sub> | -0.048 | 0.023 | -0.094 | -0.003 | 1.001     |
| <i>b</i> <sub>2</sub> | 0.318  | 0.027 | 0.264  | 0.371  | 1.001     |
| <i>b</i> <sub>3</sub> | 0.024  | 0.028 | -0.031 | 0.082  | 1.002     |
| <i>b</i> <sub>4</sub> | 0.631  | 0.025 | 0.583  | 0.678  | 1.001     |
| <i>b</i> <sub>5</sub> | 0.629  | 0.025 | 0.581  | 0.678  | 1.001     |
| <i>b</i> <sub>6</sub> | -0.050 | 0.029 | -0.107 | 0.007  | 1.001     |

Supplementary Table D2: Parameter estimates form posterior distribution for daily hoverfly species richness. *d*: climatic parameters. *c*: seasonal (quadratic effect) parameters, *b*: trap effects, and  $\log(\lambda)$ : the log-rate of decline from 1989 to 2014.

|                 | mean   | sd    | 2.5%   | 97.5%  | $\hat{R}$ |
|-----------------|--------|-------|--------|--------|-----------|
| Intercept       | 2.748  | 0.048 | 2.656  | 2.846  | 1.002     |
| $\log(\lambda)$ | -1.671 | 0.040 | -1.750 | -1.592 | 1.001     |
| $c_1$           | -0.036 | 0.033 | -0.101 | 0.029  | 1.002     |
| $c_2$           | -0.571 | 0.041 | -0.652 | -0.491 | 1.002     |
| $c_3$           | 0.325  | 0.024 | 0.277  | 0.373  | 1.001     |
| $c_4$           | -0.568 | 0.029 | -0.627 | -0.514 | 1.001     |
| $d_1$           | 0.349  | 0.019 | 0.311  | 0.385  | 1.003     |
| $d_2$           | -0.271 | 0.030 | -0.331 | -0.212 | 1.002     |
| $d_3$           | -0.010 | 0.023 | -0.054 | 0.035  | 1.001     |
| $b_2$           | 0.031  | 0.054 | -0.076 | 0.139  | 1.002     |
| $b_3$           | -0.112 | 0.053 | -0.217 | -0.009 | 1.004     |
| $b_4$           | 0.185  | 0.051 | 0.081  | 0.281  | 1.001     |
| $b_5$           | 0.117  | 0.051 | 0.019  | 0.215  | 1.003     |
| $b_6$           | -0.100 | 0.059 | -0.215 | 0.016  | 1.003     |

Supplementary Table D3: Vegetation characteristics in surrounding of trap locations. For each trap, as well as the assessed vegetative change over 25 years.

| Trap | Habitat type                              | Plant richness |      | Vegetation change and management                       |
|------|---|----------------|------|--|
|      |   | 1989           | 2014 |  |
| 1    | Nitrophilous shrub corridors, forest edge | 5              | 13   | Increase in plant diversity                            |
| 2    | Shrub corridor, wet meadow                | 28             | 16   | Improvement the diversity of plant community           |
| 3    | Perennial rich wet meadow, reedbed        | 10             | 22   | Improvement of plant diversity, and vertical diversity |
| 4    | Shrub corridor, forest edge               | 28             | 5    | Approaching richness of corridor vegetation            |
| 5    | Wet meadow, hay meadow                    | 24             | 19   | Improvement in species composition                     |
| 6    | Grassland, pasture, edge                  | 15             | 13   | Extensification of meadow use                          |





# Summary

We live in an era of biodiversity crisis, in which the rate of biodiversity loss is accelerating at an alarming rate. According to the latest global reports on the state of biodiversity, WWF report 40% of animal species face extinction, re-enforcing the proposition that we are heading towards a sixth mass extinction. Committed to preserving biodiversity, primarily for its intrinsic value, but also to safeguard ecosystem stability and the provision of ecosystem services, we are in need to establish the extent of biodiversity loss, and to uncover and elucidate the major drivers responsible. In this dissertation, long term bird and insect databases are analysed and interpreted to answer what the extent of biodiversity loss is and what the current drivers of this loss are.

Among responsible drivers, such as climate change, over-exploitation of natural resources and habitat destruction, agricultural intensification is identified to be a major contributor to biodiversity loss. In the introduction, **chapter 1**, the state of biodiversity in farmland with respect to birds and insects is briefly described, along the role that modern agricultural intensification plays in the declines of species inhabiting agricultural areas. Biodiversity in farmland appears to be more threatened than to biodiversity in natural areas. This appears to be true for at least birds, butterflies and moths, as evidenced by analysis of long term data wherever available. Application of agrochemicals and the effects on biodiversity have been known for a long time. A major class of insecticides that has been in use in the Netherlands and elsewhere from the mid 90's onward, are the neonicotinoids. Neonicotinoids have been implicated in the declines of insects, most notably bees and other pollinators, and this has been established both in experimental and empirical settings. Given their widespread use, their high toxicity and high potential for leaching in the environment, neonicotinoid contamination may cause adverse effects on insect populations, as well as all other species that rely on insects for example as a food source.

In **chapter 2**, I test the hypothesis that the spatial dynamics of insectivorous bird populations are related to neonicotinoid pesticide contamination in farmland areas. I make use of long term data on 15 common and widespread insectivorous birds in the

Netherlands, as collected by volunteers of Sovon the Dutch center for Field Ornithology, in conjunction with spatial loads of imidacloprid concentrations as collected by the Dutch Waterboard authorities. The results of this study suggest bird populations are locally experiencing lower population trends when imidacloprid concentrations in surface water are high. In addition, the pattern of bird population decline is not apparent prior to the introduction of these compounds in the Netherlands, while other potential land use drivers were inferior in explaining spatial variability in bird trends as compared to imidacloprid concentrations. Insects are indispensable to many bird species, and particularly so in the breeding season. A reduction in the insect prey base is likely to bear consequences for avian reproduction and survival, and results in lowered population trends in areas with diminished foraging resources. As neonicotinoids have been implicated in the declines of insects in contaminated surface waters in the Netherlands, we argue that a decline in insect prey base resulting from neonicotinoid contamination is the most likely mechanism explaining lowered bird trends at high neonicotinoid load in surface water.

The state of insects in the natural environment is largely unknown, but where it is known, such as for butterflies and moths, the overall pattern appears to be one of decline. Declines in insects have also been suggested as a possible cause for declines of species that rely on insects as a food source, such as insectivorous birds (e.g. as in chapter 2). However, assessing the state of insects is largely hampered by lack of large scale and long term data, and there is a need for detailed studies assessing the state of insects beyond that of only butterflies and moths. In **chapter 3** we examine long term trends in total flying insect biomass as collected with malaise traps over 27 years across 63 nature reserves in lowland Germany by the Entomological Society in Krefeld. We demonstrate that on average, the biomass of the total flying insect community has declined by 76% over 27 years, irrespective of habitat type, climatic, or landuse conditions. This loss of total insect biomass is alarming, as insects play a central role in numerous ecosystem processes, and a decline of such proportion is bound to have consequences for ecosystem functioning. The results of this study emphasize the need to uncover the geographic extent of the insect declines, and to investigate both possible causes, and ramifications of the decline.

The reported insect biomass declines in Germany, has sparked the need to increase our knowledge on the state of the insects elsewhere. In **chapter 4** we seek to establish the trends in the abundance of various insect orders in two distinct areas in the Netherlands: nature development area De Kaaistoep and nature reserves near Wijster, using two differing sampling methods: light-attraction of insects at night, and pitfall traps. Based on data from insects attracted to light in De Kaaistoep, macro-moths (macro-Lepidoptera), beetles (Coleoptera), and caddisflies (Trichoptera) have declined, while no trends were observed in other orders such as true bugs (Hemiptera: Heteroptera and Auchenorrhyncha), mayflies (Ephemeroptera) or lacewings (Neuroptera). Similar results are obtained for ground beetles (Coleoptera: Carabidae) from 48 pitfall traps near Wijster. Translated into biomass, 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. Although lower than the case of total flying insect biomass in Germany (chapter 3), our results broadly echo recent reported trends in insect biomass in Germany and elsewhere.

To what extent and in what manner the total flying insect biomass declines (Chapter 3) reflect biodiversity loss are still open questions. In **chapter 5** we analyze a dataset on the abundance and richness of hoverflies (Diptera: Syrphidae) at six locations in German

nature reserves in 1989 and 2014. This study reveals that total flying biomass reflects abundance and richness of hoverflies remarkably well, even though hoverflies represent only a minor fraction of the total insect biomass. Integrated over the two seasons, the decline in total flying insect biomass appears to be paralleled by a loss of 20% in hoverfly species richness and 80% in total hoverfly abundance over a period of 25 years. However, at the daily level, approximately 82% less species were observed, suggesting a strong temporal scaling in the local availability of hoverfly species. At the species level, almost all hoverfly species showed numerical declines. Persistence rates appeared disproportionately lower than expected for species of intermediate abundance, while the rarest species showed decline and appearance rates consistent with random expectation. Our results suggest that a common and indiscriminate factor is likely to be involved in the decline of hoverflies and possibly other insect groups. Under current threats, common and intermediately common species too, appear to be decimated in recent years.

**Chapter 6** synthesizes and integrates the findings of this dissertation with current knowledge on the effects of agrochemicals (and in particular neonicotinoids), on biodiversity, and summarizes current knowledge on the extent of insect decline, as well as potential causes and consequences of the decline. Additional research is recommended to better understand the effects of neonicotinoids on avian demography and population dynamics, as mediated through insect decline and food deprivation as result of neonicotinoid contamination. Besides indirect effects on bird populations, also direct effects of neonicotinoids on bird species have recently been described in the scientific literature, particularly for granivorous species but also predatory species, with effects ranging from mortality to disorientation during migration. Together with results of this dissertation, multiple pathways appear to exist as to how neonicotinoid usage can affect bird populations in farmland areas. However, the dramatic decline in insects populations and insect biomass over the past three decades, as described in chapters 3-5, suggests that food deprivation for insectivorous birds is likely to be an important factor, and particularly so in farmland areas. Results in this dissertation support the concerns with respect to a global biodiversity crisis, and the role of contemporary land use in declining biodiversity. Fortunately, public awareness has increased in recent years, and efforts to combat insect and biodiversity decline are underway, such as the *Deltaplan Biodiversiteit* in the Netherlands and the *Action Program for Insect Protection* in Germany, while at the European Union level, restrictions have been installed on the use of neonicotinoid insecticides in open farming systems. The exact causes of insect and biodiversity declines are yet to be established fully, and clearly more research is needed to identify and elucidate potential drivers. However, such conservation initiatives need to be implemented as soon as possible, while at the same time scientific studies should be conducted to inform conservation strategies on causes, consequences and possible solutions.



# Nederlandse Samenvatting

We leven in een tijdperk met een biodiversiteitscrisis, waarbij het huidige verlies aan biodiversiteit in een alarmerend tempo versnelt. Volgens de laatste rapporten over de staat van de wereldwijde biodiversiteit wordt 40% van de diersoorten met uitsterven bedreigd, waardoor de stelling dat we richting een zesde massale uitsterfgolf gaan niet meer hypothetisch is. Ten behoeve van het behoud van biodiversiteit, in de eerste plaats vanwege de intrinsieke waarde ervan, maar ook om de ecosysteemstabiliteit en de levering van ecosystemendiensten te waarborgen, moeten we de omvang van het biodiversiteitsverlies vaststellen en de belangrijkste drukfactoren aan het licht brengen en ophelderen. In dit proefschrift worden lange-termijn gegevens van vogels en insecten geanalyseerd en geïnterpreteerd om een antwoord te geven op de vraag wat het huidige verlies aan biodiversiteit is en wat de oorzaken van dit verlies zijn.

Naast bekende drukfactoren zoals klimaatverandering, overexploitatie van natuurlijke hulpbronnen, vernietiging van leefgebieden heeft ook de intensivering van de landbouw een belangrijke bijdrage geleverd aan het verlies van biodiversiteit. In **hoofdstuk 1** wordt de toestand van de biodiversiteit in het boerenland, meer in het bijzonder vogels en insecten, beschreven, in samenhang met de rol die de intensivering van de landbouw speelde bij de achteruitgang van deze soorten. Biodiversiteit in het boerenland is sterker bedreigd dan in natuurgebieden. Dit lijkt zeker zo te zijn voor vogels en (nacht)vlinders zoals blijkt uit een analyse van lange-termijn aantalsgegevens. De onbedoelde neveneffecten van gewasbeschermingsmiddelen op de biodiversiteit zijn al langer bekend. Neonicotinoïden zijn een groep van insecticiden die vanaf het midden van de jaren 90 in Nederland worden gebruikt. Ze blijken betrokken bij de achteruitgang van insecten, met name bijen en andere bestuivers, hetgeen zowel in experimentele als empirische onderzoeken werd vastgesteld. Gezien hun wijdverbreide gebruik, hun hoge toxiciteit en hun grote potentieel voor uitspoeling in het milieu is de hypothese gerechtvaardigd dat door verontreiniging met neonicotinoïden nadelige effecten kunnen worden verwacht op 'natuurlijke' insectenpopulaties, maar op alle andere soorten die afhankelijk zijn van insecten, bijvoorbeeld als voedselbron.

In **hoofdstuk 2** test ik de hypothese dat de ruimtelijke populatiedynamiek van insectenetende vogelpopulaties gerelateerd is aan verontreiniging met neonicotinoïden in landbouwgebieden. Er is gebruik gemaakt van lange-termijngegevens van 15 veel voorkomende en wijdverbreide insectenetende vogels in Nederland, zoals deze zijn verzameld door waarnemers van Sovon Vogelonderzoek Nederland. Dit in combinatie met een ruimtelijk beeld van de imidacloprid-concentraties zoals verzameld door de Waterschappen. De resultaten van deze studie laten zien dat vogelpopulaties lokaal lagere populatietrends ervaren met toenemende imidacloprid-concentratie in het oppervlaktewater. Bovendien is dit patroon van de achterblijvende trends van de vogelpopulaties niet aanwezig voorafgaand aan de introductie van deze pesticiden in Nederland. Ook andere landschapsveranderingen konden deze patronen in de ruimtelijke variabiliteit van vogeltrends niet verklaren. Insecten zijn onmisbaar, als voedselbron, voor veel vogelsoorten, vooral in het broedseizoen. Een vermindering van het aantal prooidieren heeft waarschijnlijk gevolgen voor de voortplanting en overleving van vogels en kan daarmee leiden tot achterblijvende populatietrends zoals we hebben geconstateerd in gebieden met een verhoogde concentratie imidacloprid in het oppervlaktewater. Niet alleen zijn neonicotinoïden betrokken bij de achteruitgang van insecten in vervuild oppervlaktewater in Nederland, ook kunnen we stellen dat het zeer waarschijnlijk is dat deze afname in een belangrijke voedselbron voor vogels geleid heeft tot het achterblijven van populatietrends ten opzichte van niet met neonicotinoïden verontreinigde gebieden.

De toestand van insectenpopulaties in hun natuurlijke omgeving is grotendeels onbekend. Voor (nacht)vlinders zijn er duidelijke aanwijzingen voor achteruitgang, maar voor andere soortgroepen betreft het slechts een vermoeden van achteruitgang. Die vermoedelijke afnames zijn ook gesuggereerd als mogelijke oorzaak voor de achteruitgang van veel soorten insectenetters (zoals in hoofdstuk 2 aangegeven). Het beoordelen van de aantalsveranderingen van insecten wordt grotendeels belemmerd door het ontbreken van grootschalige en lange-termijngegevens. In **hoofdstuk 3** onderzoek en beschrijf ik lange-termijntrends van de totale biomassa aan vliegende insecten zoals verzameld door zogenaamde malaise-vallen gedurende 27 jaar in 63 natuurreservaten in Duitsland door de Entomologische Vereniging in Krefeld. Ik toon daarbij aan dat de biomassa van de totale vliegende insectengemeenschap gemiddeld met 76% is gedaald in 27 jaar, ongeacht effecten van het weer of veranderingen in landgebruik. Dit verlies aan totale insectenbiomassa is zorgwekkend, aangezien insecten een centrale rol spelen in tal van ecosysteemprocessen en een afname met een dergelijke hoeveelheid zeker gevolgen zal hebben voor het functioneren van ecosystemen. De resultaten van deze studie benadrukken de noodzaak om op grote schaal onderzoek te doen naar de omvang van de achteruitgang van insecten en om mogelijke oorzaken en gevolgen van de achteruitgang te onderzoeken.

De gerapporteerde afnames van de insectenbiomassa in Duitsland heeft ertoe geleid dat versneld gegevens konden worden gemobiliseerd uit andere gebieden. In **hoofdstuk 4** heb ik de trends van verschillende insectengroepen in twee verschillende gebieden in Nederland vastgesteld: natuurontwikkelingsgebied De Kaaistoep en natuurreservaten in de buurt van Wijster. Deze gegevens zijn verzameld met behulp van twee verschillende bemonsteringsmethoden resp. het vangen van insecten die 's nachts aangetrokken worden tot licht op een laken en potvallen. Uit de gegevens van de De Kaaistoep, blijken macro-nachtvlinders (Lepidoptera), kevers (Coleoptera) en Schietmotten (Trichoptera) af te nemen, terwijl er geen trends werden waargenomen in andere orden zoals wantsen en cicaden (Hemiptera :

Heteroptera en Auchenorrhyncha), haften (Ephemeroptera) of netvleugeligen (Neuroptera). Vergelijkbare resultaten worden verkregen voor loopkevers (Coleoptera: Carabidae) uit de potvallen bij Wijster. Vertaald in biomassa, laten de berekeningen een reductie van de totale biomassa zien van ongeveer 61% voor macro-nachtvlinders en ten minste 42% voor loopkevers indien dit wordt geëxtrapoleerd naar een periode van 27 jaar. Onze resultaten zijn daarmee in grote lijnen in overeenstemming met recent gerapporteerde trends in insectenbiomassa in Duitsland (hoofdstuk 3) en elders.

In hoeverre en hoe de totale biomassa van vliegende insecten (hoofdstuk 3) het verlies aan biodiversiteit weerspiegelt, wordt onderzocht in **hoofdstuk 5**. Ik heb een gegevensreeks geanalyseerd van het aantal en de soortenrijkdom van zweefvliegen (Diptera: Syrphidae) op zes locaties in Duitse natuureservaten uit 1989 en 2014. Deze studie laat zien dat de totale vliegende biomassa het aantal en de soortenrijkdom van zweefvliegen opmerkelijk goed weerspiegelt, ondanks het feit dat zweefvliegen zelf slechts een kleine fractie van de totale insectenbiomassa vertegenwoordigen. Geïntegreerd over elk van de twee seizoenen, lijkt de daling van de totale biomassa van vliegende insecten gepaard te gaan met een verlies van 20% in de soortenrijkdom aan zweefvliegsoorten en 80% in het totale aantal zweefvliegen over een periode van 25 jaar. Een analyse per dag leidt tot een afname van 82% van het aantal gevangen soorten hetgeen duidt op een sterke temporele verschaling in de lokale aanwezigheid van zweefvliegsoorten. Op soortniveau vertoonden bijna alle soorten zweefvliegen een aantalsachteruitgang. Onze resultaten suggereren dat één gemeenschappelijke factor waarschijnlijk verantwoordelijk is voor de achteruitgang van zweefvliegen en mogelijk andere insectengroepen en dat nu, ook algemene soorten onder de huidige bedreigingen in gevaar zijn.

**Hoofdstuk 6** integreert de onderzoeksresultaten van dit proefschrift met de huidige kennis over de effecten van landbouwchemicaliën, met name neonicotinoïden, op de biodiversiteit, en vat de huidige kennis over de omvang van de achteruitgang van insecten samen, evenals mogelijke oorzaken en gevolgen van de achteruitgang. In dit hoofdstuk wordt ook ingegaan op de noodzaak van aanvullend onderzoek om de effecten van neonicotinoïden op de demografie van vogels en de populatiedynamiek beter te begrijpen, bijvoorbeeld het toetsen van de hypothese dat de achteruitgang van insecten als gevolg van verontreiniging van natuurlijke habitats met neonicotinoïden leidt tot voedselgebrek. Naast indirecte effecten op vogelpopulaties zijn recent ook directe effecten van neonicotinoïden op vogelsoorten beschreven, met name voor zaadetende soorten maar ook roofvogels, met effecten variërend van sterfte tot desoriëntatie tijdens de trek. Er lijken dus meerdere wegen te bestaan over hoe het gebruik van neonicotinoïden van invloed is op vogelpopulaties in landbouwgebieden. De dramatische achteruitgang van insectenpopulaties en insectenbiomassa in de afgelopen drie decennia, zoals beschreven in hoofdstukken 3-5, suggereert echter dat voedselgebrek voor insectenetende vogels een belangrijke factor is. De resultaten van dit proefschrift ondersteunen de zorgen die er zijn met betrekking tot de biodiversiteit en de rol die daarbij het hedendaags landgebruik speelt. Gelukkig is het publieke bewustzijn de afgelopen jaren toegenomen en zijn er inmiddels belangrijke initiatieven om de achteruitgang van insecten en totale biodiversiteit tegen te gaan. Belangrijk hierbij te noemen zijn het Deltaplan Biodiversiteit in Nederland en het Actieprogramma voor bescherming van insecten in Duitsland. Op internationaal niveau, de Europese Unie, zijn inmiddels beperkingen gesteld aan het gebruik van neonicotinoïden in open landbouwsystemen. Het blijft echter belangrijk de exacte oorzaken van de achteruitgang van insecten nader vast



te stellen. Er is meer onderzoek nodig om potentiële drukfactoren te identificeren en hun werkingsmechanismes te achterhalen. Initiatieven ter bescherming en verbetering van de biodiversiteit moeten echter eerder dan later worden geïmplementeerd, terwijl tegelijkertijd onderzoek plaatsvindt naar oorzaken, gevolgen en mogelijke oplossingen.

# Dankwoord

I have had an incredible time at the Radboud university, Institute of water and wetland research in Nijmegen, where I have been working on my PhD since 2012. It has been a life-changing experience, with many downs but also major ups, and with tense and exciting moments that will remain with me for the rest of my life. I would like to thank everyone who was involved during my time here at the University, as well as friends and family in private life.

Allereerst, mijn begeleiders. Het waren een zevental zeer leerzame jaren, met ontzettend spannende momenten, en ervaringen die wij vermoedelijk niet snel zullen vergeten. Hans, bedankt voor het mogen uitvoeren van een promotie-onderzoek, het vertrouwen die je me hebt gegeven om mijn ideeën uit te voeren tijdens de promotie, mentorschap, en de ondersteuning tijdens de hectische en moeilijke momenten. Ook bedankt voor de vele discussies, en vele leerzame momenten tijdens de afgelopen zeven jaar. Eelke, ik heb veel genoten van je dagelijkse begeleiding en intensieve samenwerking. Hoewel ik heel veel van je heb geleerd tijdens de afgelopen jaren, is het belangrijkste misschien wel wat het "verzilveren" van een onderzoek betekent. Ik dank je enorm voor je kritische blik, en voor het bewaken van mijn focus op momenten waar ik als ongeleid projectiel door de brede reeks aan leuke onderzoeksideeën heen schoot. Ruud, ik wil jou bedanken voor je inzet en ondersteuning tijdens mijn promotie, maar ook voor wat voorafgaande aan de promotie plaats heeft gevonden en er toe geleid heeft dat ik nu tot hier ben gekomen. Het begon ooit ik als Sovon vrijwilliger, later als junior onderzoeker bij Sovon, en toen als PhD. Bij al die stappen heb jij een grote rol in gespeeld, en al die stappen hebben mij veel kennis opgebracht, en mij doen realiseren hoe leuk onderzoek is. Ik hoop dat we nog lang door kunne sparren over mooie ideeën!

Verschillende personen hebben bijgedragen aan de totstandkoming van de hoofdstukken in dit proefschrift. Ten eerste de vrijwilligers van Sovon worden hartelijk bedankt voor hun jaren lang toewijding aan het verzamelen van vogelgegevens. Zonder hun collectieve inspanningen was het twee hoofdstuk, evenals vele andere wetenschappelijke onderzoeken,

nooit mogelijk geweest. Graag bedank ik de collega onderzoekers en veldbiologen op de Kaaistoep en in Wijster, onder andere Paul van Wielink en Henk Spijkers (KNNV Tilburg), Roel van Klink en Rikjan Vermeulen (Willem Beijerinck Biologisch Station), Theo Zeegers (EIS kenniscentrum insecten) en Jurriën van Deijk (Vlinderstichting), voor hun hulp en inzet tijdens onze prettige samenwerking. Wouter van Steenis (Natuurmonumenten) wordt hartelijk bedankt voor het mogelijk maken en ondersteunen van het onderzoek in het vierde hoofdstuk. I would like to thank the Entomological Society in Krefeld, and in particular Martin Sorg from the Entomological Society of Krefeld, for his help during my dissertation, for his long lasting devotion to field entomology, and for a very pleasant cooperation during the past several years. I hope the future brings us again to work together on the many interesting questions and challenges of entomology. Keep up the good work! All further staf of the Entomological society, including Heinz Schwan, Werner Stenmans, Andreas Müller, Hubert Sumser, Thomas Hörren, are greatly acknowledged for their contributions to the research in this dissertation. I would also like to thank Dave Goulson (University of Sussex) and Axel Ssymank (Bundesamt für Naturschutz, ) for their contributions and help during the development of the research in chapters four and five.

Graag bedank ik mijn collega's op de afdelingen in het IWWR voor de zeer prettige tijd over de afgelopen jaren. Henk, erg bedankt voor de hulp tijdens mijn promotie, de inhoudelijke goeie inzichten, en voor de mogelijkheid om het werk af te ronden bij dierecologie! Wilco, ook jij bedankt voor de inhoudelijke discussies tijdens koffiepauzes! Andy, thank you for our interesting discussions and help! Nick, Jij ook bedankt voor je inzet en bijdrage aan het tot stand komen van het derde hoofdstuk. Mijn mede-promovendi hebben voor een gezellige en prettige tijd gezorgd op de afdeling, en ik wil jullie, Marloes, Sarah Faye, Janneke, Marlous, Onno, Marloes, Anne, Eva, Laura, Maartje, Ralf, Qian, Nils, Holger, Christian, Dina, Leon, Valérie, Renske, Annieke, Natan, Jacqueline, Iris, en mijn huidige roomies Stefan en Ralph, allemaal enorm bedanken voor de interessante, mooie, leuke en inspirerende tijd. Het ga jullie goed!

Ook wil ik collega's buiten de Universiteit waar ik tijdens mijn aioschap en daarvoor mee te maken heb gehad bedanken, onder andere wie Chris van Turnhout, Henk Sierdsema, Berend Voslamber, Julia Stahl, Theo Verstrael, Frank Saris, Frank Majoor, Maja Roodbergen, Bruno Ens, Loes van den Breme, Peter de Boer, Olaf Klaasen, Christian Kampichler, Jeroen Nienhuis, Hans Schekkerman (SOVON) en Annemarieke Spitzen (RAVON), Maurice Lahaye (De Zoogdiervereniging), evenals Pascal Stroeken en Ronald van Harxen (STONE) en Henk van der Jeugd (Vogeltrekstation). Jullie allen hebben ergens bijgedragen of ondersteuning geboden, en worden daarvoor hartelijk bedankt!

Ik wil ook mijn vrienden bedanken, Wouter en Jenny, Sita en Jaap, Mike, Jasper, maar ook mensen die ik niet meer zo vaak zie, zoals Bram, Paul, Jen, Meike, Wouter M., Angelique, Sanne en Margreet. Jullie hebben, in meer of mindere mate, willens en wetens, ook van alles meegekregen van mijn leven als onderzoeker en promovendus. Jullie ondersteuning en vriendschap was daar bij van groot belang en daar wil ik jullie graag voor bedanken. Ik hoop op nog veel mooie momenten samen in de toekomst Marco, ik heb enorm veel aan je gehad, en genoten tijdens onze studies in Wageningen en tijdens de promoties in Nijmegen. Je optimisme, daadkracht, en discipline zijn een bron van inspiratie voor mij, en ik mis onze lange discussies met een glas oude whiskey of rum, en natuurlijk onze bourgondisch eten enorm! Marjolein, jij ook bedankt voor de inhoudelijke discussies in de afgelopen jaren, maar ook voor de momenten daarbuiten. Ik wens jullie allebei

het beste in Princeton, en veel succes met jullie onderzoeken daar! Επίσης θα ήθελα να ευχαριστήσω τους κουφάλες τους φίλους μου απο την Ελλάδα, και συγκεκριμένα τον Σωτήρη, Μπένη, Αλέξη και Θέμη, για την συμπαράσταση και καλοπέραση αυτά τα χρόνια. Ελπίζω στο μέλλον να βρισκόμαστε συχνότερα. Να είστε καλά!

Ook mijn familie is van groot belang geweest tijdens het promotie traject, maar vooral ook in de jaren daarvoor. Marie-Elize en Hans, jullie waren vanaf mijn eerste moment in Nederland er bij, en op vele momenten hebben jullie mij opgevangen en ondersteund! Ik dank jullie hiervoor enorm! Simon en Desire, hartelijk bedankt voor het mogen "logeren" toen ik het nodig had. Hans, Leo en Peter, ik heb veel plezier beleefd met jullie tijdens onze vogelexcursie in zeeland door de afgelopen jaren heen, en wil jullie ook bedanken voor jullie betrokkenheid en steun tijdens mijn aioschap.

Map en Pap! nou, daar ligt ie dan! Ik weet dat jullie lang niet alles, maar zeker wel heel veel mee hebben gekregen vanuit het verre Griekenland. Ik wil jullie hartelijk bedanken voor jullie ondersteuning, liefde, wijsheid en advies in de afgelopen jaren, tijdens mijn studie jaren, en natuurlijk voor alles wat daar voorafgaand is gebeurd, inclusief de stimulatie om in Nederland te gaan studeren. Ik heb van jullie geleerd de natuur te beleven en er van te houden, en dat is vrijwel zeker de belangrijkste drijfveer geweest in mijn ontwikkeling als onderzoeker en om uiteindelijk dit boekje te schrijven.

Lillie, jij hebt misschien wel het meest meegekregen, en het moeilijkst gehad, met mij als onderzoeker en promovendus. Jou steun is onmisbaar geweest in al deze jaren, en ik wil jou speciaal bedanken voor de mooie tijd, je liefde, loyaliteit, vriendschap en begrip. Ik ben erg trots op hoe wij onze wegen door het leven op onze manier uitzoeken en vinden, en ik waardeer jou enorm!

Kiddo's! Ben en Milan! ook jullie hebben vaak en lang moeten staren naar papa achter de computer, en ik wil jullie ook bedanken voor jullie geduld, liefde en steun. Jullie zijn twee geweldige kinderen, en ik leer enorm veel van jullie!

Stijntje! Ik ben erg blij dat je in mijn leven bent gekomen, en dat je het vol blijft houden ondanks al mijn tekortkomingen! Dank je voor je ondersteuning, begrip, maar vooral ook voor je liefde en gezelschap tijdens de afgelopen twee jaar! Ik kijk uit naar onze toekomst samen!



Caspar A. Hallmann

## Curriculum Vitae

Caspar Andreas Hallmann was born and raised in Rapsani, Greece, on January 11, 1983. He finished high school in Pyrgetos in 2000, after which he volunteered at the Hellenic Wildlife Hospital for approximately a year. In the period 2001-2005, he followed a Bachelors of Science study program on tropical forestry at Larenstein University of Professional Education in Velp, the Netherlands. Internships allowed him to contribute to conservation study on South Asian vultures in Punjab, Pakistan as intern at The Peregrine Fund USA, to study bird dynamics in response to overgrazing in high altitude habitats of the trans-Himalayas in India, under supervision of the Nature Conservation Foundation, India, and to study the spatial distribution of naturally occurring Mahogany populations of the Shipstern tropical forests of lowland Belize. In 2006, he pursued a Master of Science study program at Wageningen University, Wageningen, The Netherlands, on Forest and Nature Conservation, with specialization in resource ecology. During the major thesis, he studied population dynamics in fragmented populations of the Cabanis's greenbul in the Taita Hills in Kenya, in collaboration with the terrestrial ecology groups of the University of Gent, while during the minor thesis, he studied the spatial and temporal population dynamics of a recovering population of Goshawks based on long term data collected in Limburg, at Biometris Wageningen. In 2010-2011, he functioned as junior researcher at Sovon, the Dutch centre for field ornithology, where he primarily worked on developing statistical methods and tools to producing distribution and abundance maps of birds in the Netherlands. In 2012, he started a PhD at Radboud University, Nijmegen, The Netherlands, under supervision of Hans de Kroon, Ruud Foppen en Eelke Jongejans. During the PhD, he used long term and large scale datasets on insects and birds to establish the extent of biodiversity decline and to uncover potential driving factors. Caspar is a huge fan of using statistics and mathematical models to understand complex ecological processes, and to apply the models in order to inform management and conservation of natural populations. Currently, Caspar is continuing his work as researcher, and hopes he will be able to continue contributing knowledge on the state of biodiversity, and on the

eminent threats that biodiversity faces nowadays.

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## Awards

2017 Hermesdorf award major social impact research to Hans de Kroon and Caspar Hallmann

2018 Conservation Award for a scientific paper of high conservation importance 2018 by the Royal Society for the Protection of Birds.