



# Invertebrate abundance increases with vegetation productivity across natural and agricultural wader breeding habitats in Europe

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## ABSTRACT

Grassland breeding waders have been steadily declining across Europe. Recent studies indicating a dramatic decline in grassland invertebrates' abundance and biomass, the key food of most grassland wader chicks, suggest a likely driver of the demise of waders. While agricultural intensification is generally inferred as the main cause for arthropod decline there is surprisingly little information on the relationship between land use intensity and total arthropod abundance in grasslands. Here, we explored those relationships across several key wader breeding habitats by surveying ground-active, aerial and soil-dwelling invertebrate communities in five European countries that range from natural undisturbed bogs to intensively managed grasslands. Using maximum vegetation growth and soil moisture content we investigated how they shape the size of the invertebrate community within and across different countries. We found predominantly positive relationships between grassland invertebrate abundance, biomass and body weight with increasing vegetation growth and soil moisture. Maximum vegetation growth was strongly positively related to ground-active invertebrate abundance and biomass and abundance of soil dwelling invertebrates (mainly earthworms). Body weight of aerial invertebrates furthermore increased with increasing maximum vegetation growth. Our results provide little support for the hypothesis that agricultural practices associated with intensification of grassland management result in an abundance decline of invertebrate prey for wader chicks. Conservation practices aiming to enhance wader chick survival require a careful balancing act between maintaining habitat productivity to secure high prey abundance, and keeping productivity low enough to maintain open swards that do not need to be cut before chicks have fledged.

## 1. Introduction

Farmland birds are among the most rapidly declining species groups

in Europe, and conservation attempts have so far failed to halt the decline in population size and distribution (Gamero et al., 2017; Kentie et al., 2016). Changes in agricultural practices have been identified as

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the core driving factor of many species' demise with both agricultural intensification and farmland abandonment having adverse effects on farmland specialists (Benton et al., 2002; Donald et al., 2006; Durant et al., 2008; Howison et al., 2018). Ground-nesting waders are affected in particular (Siriwardena et al., 1998; Van Turnhout et al., 2010), with populations declining around 30 % solely in the last two decades (OECD and BirdLife, 2019). Low survival of wader nests and especially chicks seems to be the main factor driving wader population decline (Kentie et al., 2018; Roodbergen et al., 2012). Wader chicks of most species are precocial and forage for arthropods and other invertebrates such as earthworms or leatherjackets from the moment they hatch (Beintema et al., 1991), with particularly large arthropods being important because these are energetically the most rewarding (Schekkerman and Beintema, 2007).

Recent studies suggest that arthropod abundance and biomass in European grasslands have dramatically declined (Hallmann et al., 2017, 2019; Seibold et al., 2019) and that this may drive declines of higher taxa that depend on them (Goulson, 2019; Lister and Garcia, 2018). Some studies furthermore report that large species have become smaller over time (Oliveira et al., 2016). It is commonly accepted that arthropod declines are largely the result of changing, more intensive agricultural practices (Møller, 2019; Raven and Wagner, 2021; Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019), and interactions with future climate scenarios may potentially exacerbate abundance declines (Sohlström et al., 2022). However, the negative effect of farming is often implied from a lack of a relationship with other explanatory variables (Hallmann et al., 2017; Seibold et al., 2019).

While there is convincing evidence that farming practices can negatively affect specific species groups such as bees, carabids or spiders (Blake et al., 1994; Bell et al., 2001; Ekroos et al., 2020) there is surprisingly little information on the relationship between land use intensity and total arthropod abundance, arguably the most relevant variable for arthropod-feeding farmland birds. A notable exception is Benton et al. (2002) who found, in a mixed farming system, a decline in invertebrate abundance with increasing farming intensity over time, which was correlated to a decline in farmland birds. However, not all agricultural practices are expected to adversely affect arthropod abundance. Grassland intensification typically involves increasing the vegetation quality and productivity through improving drainage, application of fertilizers or correcting soil properties that impede plant growth. Experimental fertilization studies often show an increase in arthropod abundance caused by increased quantity and/or quality of the vegetation (Haddad et al., 2000; Siemann, 1998; Vince et al., 1981). Empirical studies that examine arthropod communities under different regimes of agricultural management indeed show varying results. For example, Dennis et al. (2007), finds that important bird arthropod prey abundances decreases with increasing grazing intensity in Scottish moorland. Simons et al. (2014) finds that the herbivore arthropod community biomass and abundance in German semi-natural grasslands does not significantly differ in contrasting fertilizer application rates. Kleijn et al. (2010) finds positive relationships between total arthropod abundance and fertilizer input in Dutch meadow bird grasslands.

However, these studies only provide partial insight in the relationship between farming intensity and arthropod communities because they examine effects of manipulating the management of existing, often intensive, farming systems. In such studies, long-term and large-scale effects of, for example, past fertilizer applications, modifications in the regional hydrology or nitrogen deposition may partially mask relations between arthropod numbers and land-use intensity. This makes it difficult to assess whether, and under what conditions, arthropod availability is a key limiting factor for wader chick survival, or whether other processes play a more dominant role, such as mortality caused by mowing machinery (Schekkerman et al., 2009), too dense swards making the available arthropods inaccessible (Kleijn et al., 2010) or mowing-induced lack of cover leading to enhanced chick predation rates (Schekkerman and Beintema, 2007).

Here we use an alternative approach to assess the relationship between land use intensity and arthropod abundance in wader habitats. We make use of the natural variation in land-use intensity that is still present in Europe and survey the range of key breeding wader habitats from no-input natural habitats such as mires and bogs to intensively managed high-input grasslands. We sampled aerial, ground-active and soil-dwelling invertebrates in 64 sites in five countries and related their abundance, biomass and average individual body weight to vegetation productivity (used as a proxy for land-use intensity) and soil moisture content as key variables affecting wader chick habitat quality. We test whether invertebrates decline with increasing land use intensity, which would support the hypothesis that intensive farming practices are a key driver of invertebrate prey. We also examine whether and how invertebrates are affected by soil moisture content, a key variable for many wader species as it affects the ability of adult birds to probe the soil for invertebrate prey (Korniluk et al., 2021; Smart et al., 2006; Struwe-Juhl, 1995) and known to influence vegetation productivity (Heisler-White et al., 2009).

## 2. Methodology

### 2.1. Study sites and design

Data was collected in 64 sites in five countries across mainland Europe: France, the Netherlands, Poland, Estonia and Finland. To standardize habitat types and to make sure that results would be relevant for wader conservation, all sites had been hosting breeding waders (particularly the near-threatened black-tailed godwit *Limosa l. limosa*; BirdLife International, 2017) in the years before sampling, as indicated by local experts. Eighty-one per cent of the sites hosted black-tailed godwit territories in the year we surveyed these sites, all contained at least one territory of a wader species and breeding densities varied substantially (Table 1). The relationship between environmental variables, invertebrate abundance and black-tailed godwit breeding densities is topic of another paper (Silva-Monteiro et al. in prep.) and will not be addressed here. We aimed to include sites that varied as much as possible in land-use intensity both within countries and between countries, and sampled bogs and fens (natural habitats with no agricultural use), coastal and floodplain grasslands (semi-natural habitats that are grazed or mown but do not receive any inputs) and improved grasslands varying in management intensity (none to high fertilizer input; see Supplementary information Table S1 for more detailed information). Each site was sampled in a single season which was timed to start approximately three weeks prior to the estimated mean hatching date of black-tailed godwit chicks (roughly between April and June) and the sampling period covering 48 and 72 days, depending on country. Logistical constraints forced us to sample different countries in different years with sites in Finland being sampled in 2017, sites in Estonia both in 2017 and 2018, France and the Netherlands being sampled in 2018 and the Polish sites being sampled in 2019. Sites were located a minimum of 0.5 km apart ensuring they represented independent observations.

### 2.2. Invertebrate sampling

In each site, we surveyed aerial, ground-active and soil-dwelling invertebrates, sampled vegetation biomass and measured soil moisture content at twelve-day intervals throughout the local wader breeding season (see Supplementary information Fig. S1 for a visual concept of the sampling methods). Each site had a total of four to six sampling rounds. Four rounds only occurred when individual sites were inaccessible due to flooding in the first sampling round. Only the French sites were sampled six times by extending the sampling period with one more survey round. Because black-tailed godwit, and other wader species' chicks are considered opportunistic feeders, foraging all available arthropod orders (Beintema et al., 1991; Johansson and Blomqvist,

**Table 1**

A summary of the observed invertebrate numbers and the main explanatory variables (maximum vegetation growth rate and soil moisture) per broad habitat type and country (mean  $\pm$  s.e.). Habitat types are ordered from low- to high-intensity. Observed settlement densities of black-tailed godwits and the wader community at large are also given for reference. See for survey methodology of waders Silva-Monteiro et al. (in prep.).

Habitat type - country	Maximum vegetation growth (g.m <sup>-2</sup> .day <sup>-1</sup> )	Soil moisture (%)	Invertebrate abundance			Black-tailed Godwits territories (100 ha <sup>-1</sup> )	Total wader territories (100 ha <sup>-1</sup> )
			Ground-active	Aerial	Soil-dwelling		
Bogs and fens Estonia (n = 7)	3.8 $\pm$ 1.3	99.1 $\pm$ 0.9	32.3 $\pm$ 5.1	1103.1 $\pm$ 271.6	0.0 $\pm$ 0.0	1.8 $\pm$ 0.5	4.1 $\pm$ 1.1
Floodplain meadows Estonia (n = 2)	15.5 $\pm$ 4.0	53.5 $\pm$ 12.3	93.5 $\pm$ 7.5	1187.0 $\pm$ 433.0	0.0 $\pm$ 0.0	0.7 $\pm$ 0.7	1.4 $\pm$ 1.4
Poland (n = 5)	8.0 $\pm$ 2.0	50.5 $\pm$ 4.3	193.0 $\pm$ 29.6	1191.0 $\pm$ 116.6	3.0 $\pm$ 1.0	4.0 $\pm$ 4.0	18.6 $\pm$ 11.2
Coastal meadows Estonia (n = 7)	13.2 $\pm$ 2.9	38.2 $\pm$ 1.8	99.4 $\pm$ 15.0	810.6 $\pm$ 81.9	0.1 $\pm$ 0.1	8.9 $\pm$ 2.6	19.6 $\pm$ 4.1
Finland (n = 6)	4.0 $\pm$ 0.9	58.0 $\pm$ 5.6	39.3 $\pm$ 6.9	1459.2 $\pm$ 473.2	0.3 $\pm$ 0.3	16.8 $\pm$ 5.8	38.6 $\pm$ 11.5
Extensive meadows Poland (n = 6)	6.3 $\pm$ 0.9	67.0 $\pm$ 1.8	95.3 $\pm$ 9.1	1339.0 $\pm$ 276.8	1.2 $\pm$ 0.7	18.2 $\pm$ 9.4	32.7 $\pm$ 8.2
France (n = 12)	14.9 $\pm$ 2.1	22.7 $\pm$ 0.8	222.6 $\pm$ 26.5	445.4 $\pm$ 38.5	1.8 $\pm$ 0.2	5.7 $\pm$ 1.6	17.5 $\pm$ 3.2
Netherlands (n = 4)	10.4 $\pm$ 3.2	34.6 $\pm$ 4.7	328.8 $\pm$ 51.8	2083.3 $\pm$ 122.8	20.3 $\pm$ 2.5	145.9 $\pm$ 42.5	252.1 $\pm$ 60.4
Intensive meadows Finland (n = 7)	7.2 $\pm$ 1.9	30.1 $\pm$ 2.9	34.4 $\pm$ 8.3	377.6 $\pm$ 167.2	0.0 $\pm$ 0.0	18.2 $\pm$ 5.6	40.2 $\pm$ 17.0
Netherlands (n = 8)	16.4 $\pm$ 2.5	39.4 $\pm$ 3.5	442.9 $\pm$ 83.8	1511.9 $\pm$ 174.3	11.3 $\pm$ 2.0	62.5 $\pm$ 11.3	115.2 $\pm$ 21.6

1996; Schekkerman and Beintema, 2007), we considered all sampled arthropods as relevant prey items.

Arthropods (insects and spiders) were sampled using a combination of pitfall traps and sticky traps (Eglington et al., 2010). Aerial insects were surveyed using three yellow sticky boards (10  $\times$  25 cm, adhesive on two sides; brand Koppert, type Horiver) per site and survey round, placed vertically in the vegetation with the bottom end approximately 10 cm above ground surface and spaced 10 m apart. After four days, the traps were removed and individual arthropods counted. The abundance of the ground-active arthropods was estimated by means of three pitfall traps (plastic yoghurt cups, height 125 mm and diameter 85 mm) spaced 10 m apart, that were filled with water and cooling fluid to act as a preservative. A cover raised 60 mm above the pitfall traps protected them from flooding during rainfall. Pitfall traps were open for four days per sampling period and closed with a lid for the remaining eight days of the twelve-day period. Both ground and aerial arthropods were identified to order and categorized in four size classes according to their body length: 0–2, 2–4, 4–10 and  $\geq$ 10 mm. Arthropod biomass (mg) was estimated for each order and size class by means of length-weight formulas available in Rogers et al. (1976, 1977). We used 1 mm for the “0–2 mm” size class, 3 mm for the “2–4 mm”, 7 mm for the “4–9 mm” and 10 mm for the “ $\geq$ 10 mm” class. Average individual body weight (mg/individual) was calculated by dividing the sum of all size classes' biomasses with the total abundance of arthropods.

Soil-dwelling invertebrates, primarily earthworms and leatherjackets (Tipulidae larvae) were surveyed by extracting 20 cm wide by 20 cm long by 15 cm deep soil samples from each site using a spade (Kleijn et al., 2011). Because soil macro-fauna is not expected to change much over the season, sampling was done only twice during the breeding season, simultaneously with the first and last arthropod samples. In each field, five samples were taken randomly located in the same general location of the arthropod samples. Per site and sampling round, the pooled number of earthworms and leatherjackets were counted on site by manually inspecting the extracted soil sample and expressed in

number of individuals per m<sup>2</sup>. Soil-dwelling invertebrate abundance was expressed as the average of the two sampled rounds.

### 2.3. Surveying environmental variables

Vegetation biomass (dry weight in g/m<sup>2</sup>) was estimated by clipping the vegetation in three 30  $\times$  30 cm vegetation plots randomly located within 10 m of the arthropod sampling sites and weighing them after drying for two days in an oven at 70 °C. To determine soil moisture content (%), five 15 cm deep soil samples located randomly in the same general vicinity as the biomass samples were taken using an auger (or soil corer). Subsamples were pooled and mixed and fresh weight was determined after which samples were dried at 105 °C for 12 h in order to determine their dry weight. Soil moisture content in percentage was calculated as  $(([\text{soil fresh weight} - \text{soil dry weight}] / \text{soil fresh weight}) * 100)$ .

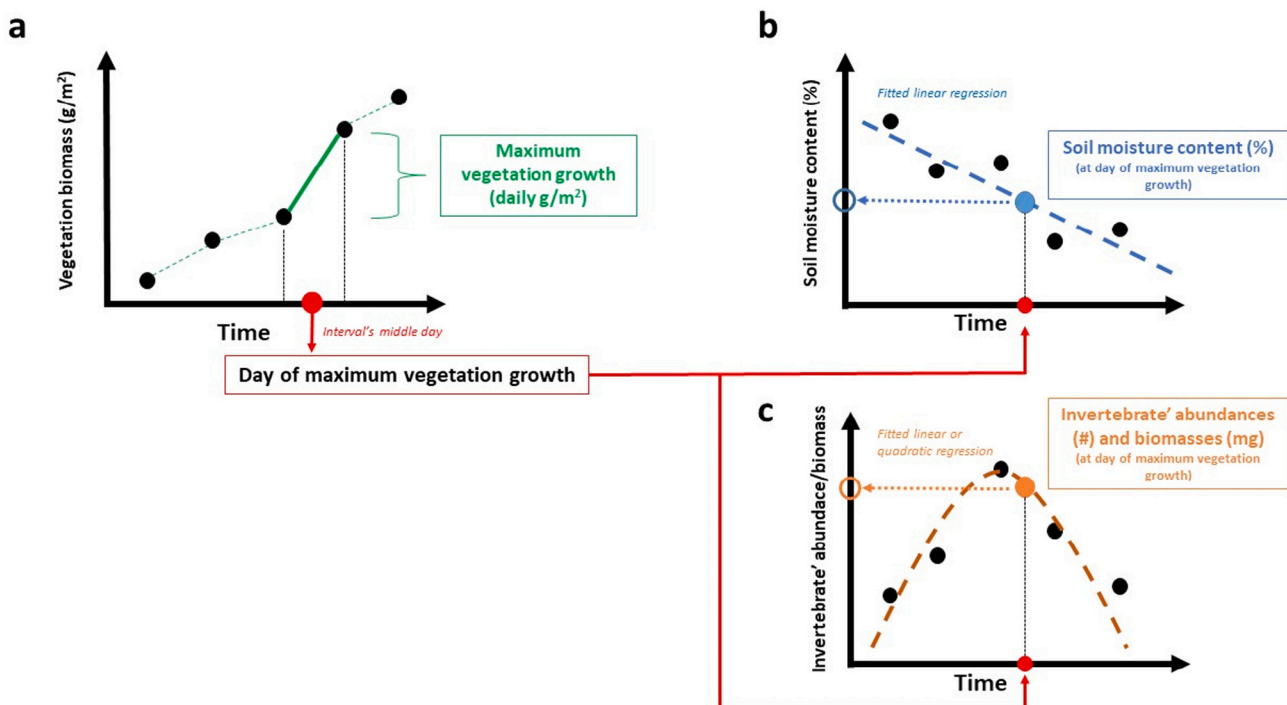
We used temperature sums (Tsum; Prins et al., 1988) to correct for the unavoidable differences in phenology of the vegetation and arthropod communities caused by sampling sites with different management (see analysis framework below). Arthropod development, like vegetation growth, is strongly influenced by temperature (Logan et al., 2006; Ratte, 1984). If sites were grazed or mown before maximum vegetation growth could occur, estimates would be expected to occur at a lower Tsum than undisturbed sites in the same country. Including Tsum in the analyses could therefore account for part of the environmental noise caused by management differences. Tsums were calculated by summing the daily average temperatures above 0 °C starting on January 1st until the maximum vegetation growth day. Daily average temperatures were extracted from the Global Historical Climatology Network (Menne et al., 2012) using a nearby meteorological station where complete datasets were available.

## 2.4. Analytical framework

Our study included sites that did not receive external inputs or were even entirely unmanaged by people making it difficult to use commonly input-based indicators of land-use intensity such as nitrogen input or grazing intensity (Herzog et al., 2006; Kleijn et al., 2009a,b). We therefore used maximum vegetation biomass growth as an indicator of land-use intensity as this reflects the outcome of all management practices implemented by farmers to enhance productivity. This has the added benefit that it also incorporates natural variation in productivity that may affect arthropod communities. In each site, maximum vegetation biomass growth was estimated as the largest increase between two successive biomass samples and dividing the difference by the number of days in between (daily  $\text{g}/\text{m}^2$ ; Fig. 1a). Because the vegetation in bogs (surveyed only in Estonia) did not demonstrate any clear peaks in biomass production, for bog sites we used the average growth rate across the entire sampling period as maximum growth rate. We subsequently used the median day of the sampling interval with maximum vegetation growth to standardize our estimates of the other environmental variables and the arthropods (Fig. 1). For soil moisture content, we fitted linear relationships with time and used the model predicted value at the median day of maximum vegetation growth as our estimate of soil moisture content (Fig. 1b). The advantage of using this approach is it uses data from all our samples, thus reducing the impact of outliers. We followed the same approach for the arthropod sampling but here we used a linear or quadratic regression (best fit visually selected) from the sampled replicas (Fig. 1c). For the bog sites in Estonia, for which maximum vegetation growth estimates were based on the entire sampling period rather than an individual sampling interval (see above), we used the average date of maximum vegetation growth in coastal and floodplain meadows that were sampled in the same year to extract corresponding arthropod, soil moisture and temperature sum data.

## 2.5. Statistical analyses

We employed generalized linear mixed models and an information theoretic approach to investigate to which extent the selected environmental explanatory variables drive the arthropod community's abundances, biomass and average individual body weight. We used country as a random variable and applied the “within-subject centering” procedure (van de Pol and Wright, 2009) in order to disentangle effects of the explanatory variables within and between countries. To do this, we first scaled and centered the explanatory variables (maximum vegetation growth, soil moisture content and Tsum) through the whole dataset in order to observe potential within country relations (referred to as ‘explanatory variable – within’). We then scaled and centered the country's averages of maximum vegetation growth and soil moisture content in order to observe potential relations across countries (‘explanatory variable – across’). In our model selection approach, we forced the predictor Tsum-within to be included in all models to account for effects of local differences in mowing and grazing practices that were outside the scope of the study. Interactions between explanatory variables in the models were not considered due small sample sizes among countries as the analyses across countries are being done on the basis of a single mean value per country. Negative binomial and gamma distributions (with log-link) had the best data fitting and were thus used for abundance and biomass/average individual body weight respectively. Careful inspection of residuals, suggested none of the models was zero-inflated or suffered from over- or under-dispersion. We used an all-subsets approach to build a model set containing all possible combinations of the different explanatory variables. Individual models were restricted to have a maximum of three explanatory terms, in addition to Tsum-within, to avoid overfitting in view of sample size (Babyak, 2004). We used the Akaike information criterion corrected for small sample size (AICc) to select models that had a  $\Delta\text{AICc} < 2$  (Burnham et al., 2011). Full-model averaged parameter estimates (comprising zeroes when the predictors were not present in certain models) were calculated for each predictor in the model set (Symonds and Moussalli, 2011). This



**Fig. 1.** Methodological process for obtaining each sites' representative environmental explanatory variables (maximum vegetation growth in green, soil moisture content in blue) and respective invertebrate community response variables (in orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



approach allowed us to compare the relative importance of different predictor variables because standardized effect sizes of different predictor variables can directly be compared and the 95 % confidence intervals of effect sizes can be used to assess their reliability. All analyses were performed in R (R Core Team, 2017), using packages glmmTMB (Brooks et al., 2017) and Mu-MIn (Barton, 2020).

### 3. Results

#### 3.1. Differences between habitat types and countries

A number of variables indicated the expected patterns (Table 1). For example, bogs and fens had the highest mean soil moisture content and agricultural grasslands had the lowest. Soil dwelling invertebrates only occurred in considerable numbers in the relatively intensively managed Dutch sites and to a lesser extent in the Polish floodplain meadows. In a number of other habitat types they were completely absent. However, for the other variables there was considerable variation in the response and explanatory variables both between the habitat types, within countries and within habitat types between countries with no obvious patterns. Across all investigated habitats and countries, the variables showed four- to 13-fold increases from lowest to highest values (Table 1), indicating that sufficient variation was present for doing meaningful analyses on the relationship between response and explanatory variables.

#### 3.2. Factors related to ground-active invertebrates

In total, we counted 42,968 ground-active, invertebrates. The model averaged estimates of the variables included in the candidate model set ( $\Delta AIC_c < 2$ ) suggest that maximum vegetation growth across countries was most strongly related to the abundance of ground-active invertebrates (Table 2). This relationship shows a nearly fourfold increase in abundance between the near-natural sites with the lowest maximum vegetation growth in Finland and Poland and sites with the highest productivity in the Netherlands and France (Fig. 2a). There were only two models in the candidate set of best models, both featuring positive relations with vegetation growth within and/or across countries (Supplementary information Table S2). Maximum vegetation growth across countries also had the highest averaged estimate ( $\beta = 0.43$ ) for ground-active invertebrate biomass. However, the 95 % confidence interval of the estimate overlapped zero indicating more uncertainty for biomass than for abundance. All other examined explanatory variables also featured in the candidate model set, but in contrast to maximum vegetation growth, estimates were close to zero, indicating low relative importance (Table 2). The correcting variable Tsum-within was however consistently positively related to ground active invertebrates ( $\beta = 0.18$ , 95 % CI not overlapping zero). Average body weight of invertebrates was most strongly related to soil moisture within countries (Table 2, Fig. 2b) with positive relations across a wide range of soil moisture

content (Fig. 2b).

#### 3.3. Factors related to aerial invertebrates

We counted a total of 264,565 aerial invertebrates. The abundance of aerial invertebrates was not well explained in our study with none of the variables having high effect sizes and all 95 % confidence intervals overlapping zero. Similarly, aerial invertebrate biomass was not strongly related to productivity indicators or soil moisture with the correcting variable Tsum-within having the highest averaged estimate ( $\beta = 0.34$ ; 95 % CI not overlapping zero). However, the best candidate model set for aerial invertebrate average body weight consisted of a single model (Supplementary information Table S2) that indicated consistent and pronounced positive relationships with both vegetation growth across and within countries (Table 2). Both across and within countries aerial invertebrate body weight increases almost threefold from low to high maximum vegetation growth (Fig. 3a and b respectively).

#### 3.4. Factors related to soil dwelling invertebrates

In total 478 soil-dwelling invertebrates were observed. The abundance of soil dwelling invertebrates such as earthworms was positively related with maximum vegetation growth across countries. Effect size was relatively high ( $\beta = 0.47$ ; second highest of all effect sizes) with a predicted increase from 0.05 to 0.73 individuals per square meters across the observed range of maximum vegetation growth rate (Fig. 4). However, many soil samples did not contain any earthworms and the large number of zeros may explain why the 95 % confidence interval was so large and included zero. The negative effect size of soil moisture content across countries may have been relatively unreliable for similar reasons.

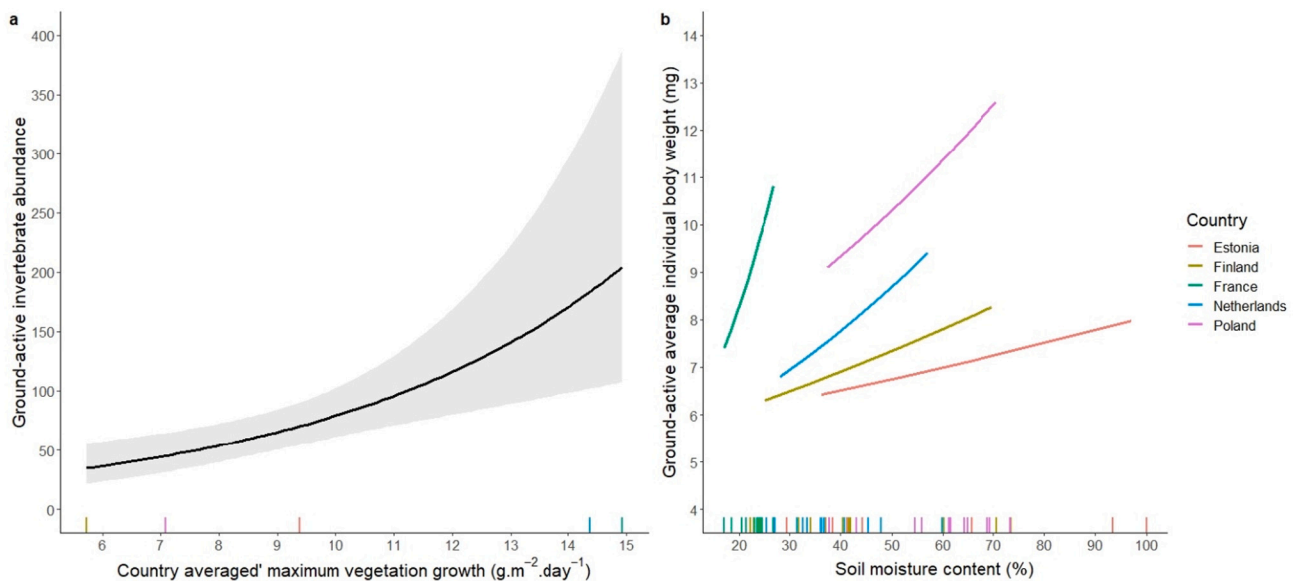
### 4. Discussion

Across a wide range of wader habitats that spans from waterlogged natural low-productive bogs and fens all the way to heavily drained high-input agricultural grasslands, our results show predominantly positive relationships between grassland invertebrate abundance, biomass and body weight on one hand and maximum vegetation growth and soil moisture on the other hand. This implies that drainage of (semi-) natural wader habitats may result in a decline in the size of ground-active invertebrates but at the same time the much larger effect sizes of maximum vegetation growth on a number of different invertebrate parameters suggests that practices aimed to increase vegetation productivity will enhance grassland invertebrates overall. Our results therefore provide little support for the hypothesis that agricultural practices associated with intensification of grasslands by definition result in a decline in the abundance of arthropods and therefore in the potential availability of invertebrate prey for wader chicks.

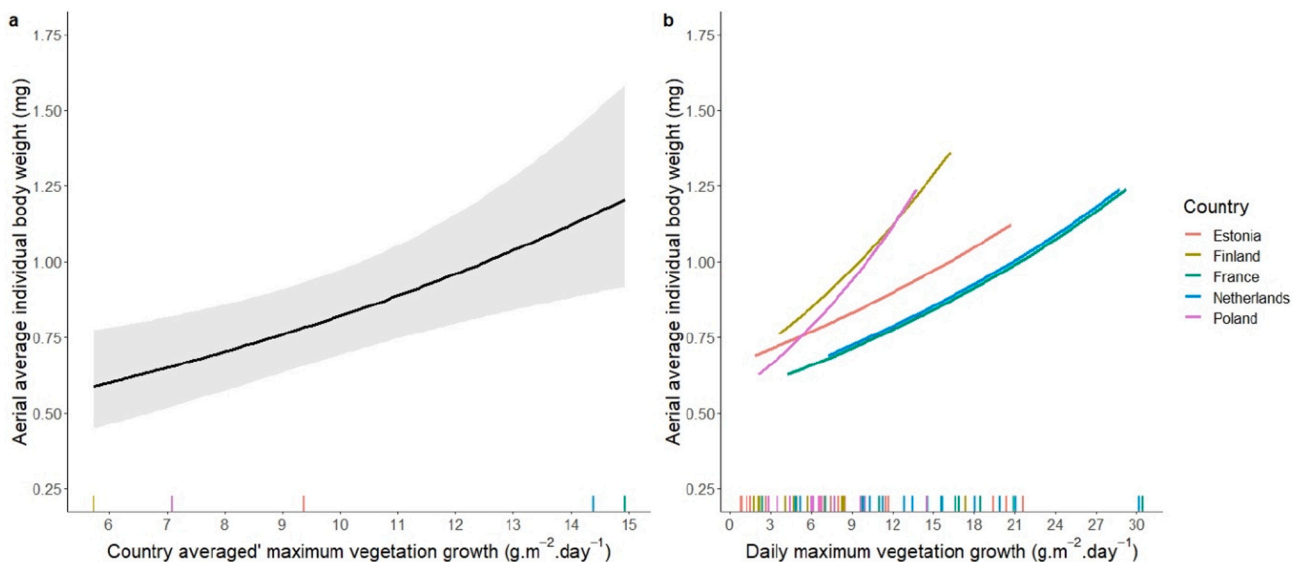
**Table 2**

Model-averaging results of the candidate model sets explaining abundance, biomasses and average individual body weight (AIBW) of ground-active, aerial and soil-dwelling invertebrates. For each predictor, the model-averaged parameter estimate ( $\beta$ ) is given, followed by its 95 % confidence interval (CI), indicated in bold when not overlapping zero.

	Vegetation growth within	Vegetation growth across	Soil moisture content within	Soil moisture content across	Temperature sums within
Ground-active					
Abundance	0.04 (−0.09–0.18)	<b>0.71 (0.30–1.12)</b>			0.10 (−0.04–0.24)
Biomass	0.01 (−0.07–0.09)	0.43 (−0.35–1.21)	0.02 (−0.08–0.11)	0.03 (−0.29–0.34)	<b>0.18 (0.02–0.34)</b>
AIBW	0.00 (−0.04–0.04)	−0.02 (−0.14–0.10)	<b>0.11 (0.03–0.19)</b>	0.06 (−0.14–0.26)	0.08 (0.00–0.16)
Aerial					
Abundance	−0.10 (−0.26–0.06)		0.05 (−0.09–0.19)	0.03 (−0.17–0.23)	0.14 (−0.02–0.30)
Biomass		0.13 (−0.36–0.62)	0.02 (−0.10–0.14)	0.07 (−0.10–0.14)	<b>0.34 (0.14–0.54)</b>
AIBW	<b>0.21 (0.05–0.37)</b>	<b>0.29 (0.11–0.47)</b>	−0.02 (−0.14–0.10)		0.10 (−0.07–0.28)
Soil-dwelling					
Abundance		0.47 (−0.94–1.88)		−0.23 (−1.37–0.91)	0.00 (−0.23–0.24)



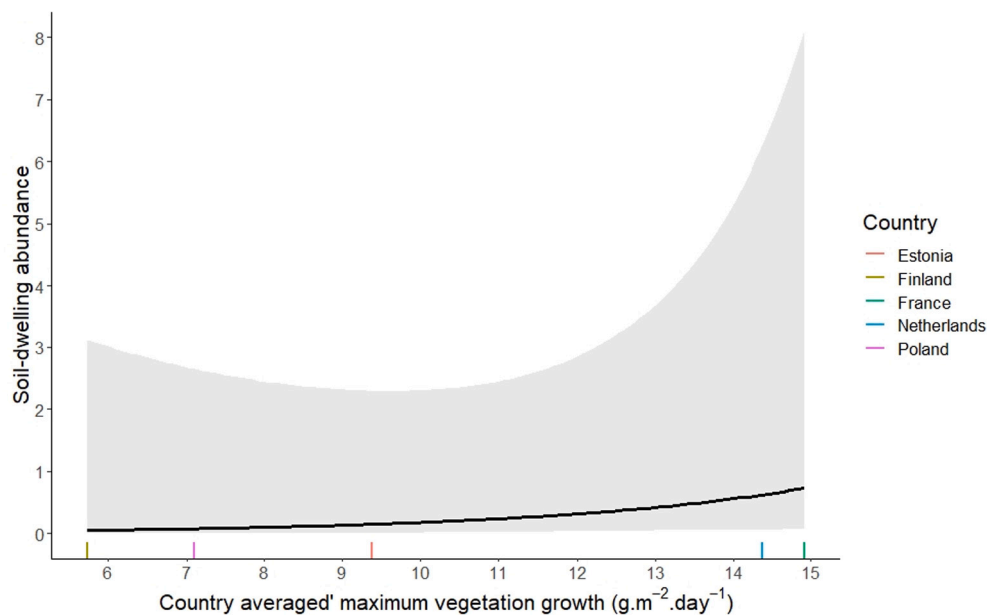
**Fig. 2.** The relationships of ground-active invertebrate abundance with vegetation growth across countries (a) and ground-active invertebrate average individual body weight with soil-moisture content within countries (b). Regression plots are based on models with all explanatory variables present in the averaged model from the candidate model set. Light grey band in panel a displays 95 % confidence interval for the shown across-country relationship. Confidence bands are not presented in panel b to avoid unnecessary visual overlapping. Rugs at the bottom of the figure indicate the x-value for the partial residuals.



**Fig. 3.** The relationships of aerial invertebrate average individual body weight with vegetation growth across (a) and within countries (b). Regression plots based on models with all explanatory variables present in the averaged model from the candidate model set. Light grey band in panel a displays 95 % confidence interval for the shown across-country relationship. Confidence bands are not presented in panel b to avoid unnecessary visual overlapping. Rugs at the bottom of the figure indicate the x-value for the partial residuals.

The observed predominantly positive relationships between invertebrates and vegetation growth are in line with the theory of cascading effects of nutrient availability on arthropods through plant biomass and quality (Andrey et al., 2014; Haddad et al., 2000; Siemann, 1998). Living and dead plant tissue is, either directly or indirectly through consumption of other invertebrates, the primary food source for most invertebrates. It is therefore perhaps not surprising that the size of the invertebrate communities increases with habitat productivity because more productive habitats simply provide more resources to sustain invertebrates. Andrey et al. (2014), observed a marked increase in arthropod abundance after experimentally increasing the productivity of nutrient-poor grasslands. Our study observes a similar trend using a correlative approach that examines invertebrates in habitats with

contrasting productivity. The disadvantage of our approach is that we did not study the impact of vegetation productivity under standardized biotic and abiotic conditions. This was inevitable, because a key objective of our study was to better understand how land-use intensity affects the abundance of invertebrate prey for wader chicks, and natural and intensively farmed wader habitats generally do not occur within close proximity of one another. The fact that our study found relatively clear patterns for ground-active invertebrates despite the environmental differences between habitats suggests a robust relationship between habitat productivity and population size of ground-active invertebrates such as beetles, spiders and ants that are generally caught with pitfall traps. The much wider range in observed maximum vegetation growth across countries than within countries, could explain why relationships



**Fig. 4.** Soil-dwelling invertebrate abundance relationship with vegetation growth across countries. Regression plots based on model with all explanatory variables present in the averaged model from the candidate model set. Light grey band displays 95 % confidence interval for the shown across-country relationship. Rugs at the bottom of the figure indicate the x-value for the partial residuals.

across countries were generally more pronounced than relationships within countries (Table 2).

Soil moisture did not show clear relationships with invertebrate abundance or biomass. Only body weight of ground-active invertebrates was clearly positively related to soil moisture within countries (Fig. 1b). Little is known about how soil-moisture conditions influence invertebrate size (Smith et al., 2009) but the few available studies suggest that smaller body size does correlate with drier soils in some species of invertebrates (Huk and Kühne, 1999; Vessby, 2001). Invertebrate abundance and biomass has been found to be positively related to soil moisture and presence of wet features, such as foot drains or pools (De Felici et al., 2019; Eglington et al., 2010). Invertebrates generally prefer to oviposit in moist locations where larval development is often more successful (Huk and Kühne, 1999; Knisley et al., 2018). Our study was done in wader habitats, which are generally rather wet, particularly in the (near-)natural sites. A possible explanation for the absence of a relationship with soil moisture in our study, could be that this was only a limiting factor for invertebrate abundance and biomass in the driest sites in France, the Netherlands and Finland (Fig. 2b). Because our sampling size did not allow for a reliable analysis of the interaction between maximum vegetation growth and soil moistures we could not actually test this. However, a clear conclusion is that, within wader habitats, productivity is a stronger driver of invertebrates than soil moisture.

The lack of an association of aerial invertebrate abundance or biomass with any predictor might originate from the sampling method that we used. Unlike pitfall traps, that generally sample specimens from the same area where vegetation growth and soil moisture were sampled (Elek et al., 2014), sticky traps sample invertebrates that may have come from much farther distances (Taylor et al., 2010). The larvae of many aerial insects, particularly of the Diptera that are often well-represented on sticky traps (Whitaker et al., 2000), develop in water bodies (Thorp and Rogers, 2011), which are unrelated to the site characteristics as measured in our study. Yellow sticky traps furthermore sample pollinators (Wheelock and O'Neal, 2016) that are related to landscape-level factors as well as local factors (Steffan-Dewenter et al., 2002). In our study, the characteristics of the landscapes surrounding the sampled sites may therefore have been more important than the local site conditions for aerial invertebrate abundance and biomass. Nevertheless, body weight of aerial invertebrates showed clear and consistent positive

relations with both vegetation growth within and across countries (Table 2, Fig. 3), which is in line with previous findings in Dutch wader grasslands (Kleijn et al., 2009a,b). Body size increases of important grassland invertebrates such as crane flies have been linked to increases in habitat productivity before (Jourdan et al., 2019). However, why we found clear relationships between local productivity indicators and body weight but not with invertebrate abundance and biomass remains puzzling.

Soil-dwelling invertebrates are occasional prey for precocial wader chicks (Beintema et al., 1991; Schekkerman and Beintema, 2007) but are the main food source of many adult breeding waders (Buchanan et al., 2006). Our results indicate that soil-dwelling invertebrates tend to increase primarily with increasing productivity of sites. Uncertainty of the relationship was large, probably because of a complete lack of soil-dwelling invertebrates, mainly earthworms, in most sites in Finland and Poland (Fig. 4). The increase in earthworm abundance in more productive sites is most likely linked to fertilizer application as earthworm densities generally increase with pH and fertilizer application (Atkinson et al., 2005). This result suggests that productive habitats provide food for both adults and chicks (Beintema and Visser, 1989; Ewing et al., 2018). Unproductive habitats, on the other hand, only provide food for chicks so that adult birds have to forage on neighboring sites that are more productive (Struwe-Juhl, 1995).

Our study sheds more light on the current debate on the causes of insect decline. There is convincing evidence that agricultural intensification has negative effects on a wide range of invertebrate groups (Benton et al., 2002; Ekroos et al., 2020). However, our results indicate that generalist invertebrates that make up the bulk of insect biomass may actually benefit from agricultural practices aimed to enhance the productivity of grasslands. This is in line with a recent study showing that abundance of aquatic invertebrates in the Netherlands has declined over the past three decades because of reduced nitrogen and phosphorus concentrations in surface water while taxonomic diversity increased over the same period (Hallmann and Jongejans, 2021). Unlike arable crops, even improved grasslands are only rarely treated with insecticides, which may allow saprophytic and herbivorous insects to build up substantial populations. Although our study did not determine whether peaks in invertebrate availability match the main chick foraging period or whether invertebrate availability was enough to meet

wader chick energy demands (Meltøfte et al., 2007; Tulp and Schekkerman, 2008), these results suggest that lack of invertebrate prey is probably not the main driver of the high grassland wader chick mortality observed on intensively managed grasslands. This is further supported by findings that the growth rate of black-tailed godwit chicks does not differ between medium and high-intensity grasslands (i.e. herb-rich grasslands with foot drains vs. monocultures; Loonstra et al., 2017).

Our results indicate that the abundance of invertebrate prey of wader chicks increases with increasing land-use intensity. We do, however, not recommend unconstrained intensification of management of wader habitats to enhance chick prey availability. Studies from Northwestern Europe show clear negative effects of agricultural intensification on both wader breeding population densities (Douglas et al., 2021; Jóhannesdóttir et al., 2019; Silva-Monteiro et al., 2021) and wader chick survival (Roodbergen et al., 2012) through mechanisms other than food abundance, such as more difficult access to invertebrate prey in dense, heavily fertilized swards (Kleijn et al., 2010), higher mortality rates due to more frequent agricultural activities or higher exposure to predators in recently cut vegetation (Kentie et al., 2015; Loonstra et al., 2019; Schekkerman and Beintema, 2007). Conservation practices aiming to enhance wader chick survival therefore requires a careful balancing act of maintaining habitat productivity to provide enough prey for chicks, and possibly adult birds, while keeping productivity low enough to maintain open swards that do not need to be cut before chicks have fledged.

#### CRedit authorship contribution statement

MSM and DK conceived the ideas and designed methodology; MSM, HP, ST, JP, EP, MV, JL, FR, MK, PS, MO, AD, MB, JH, SB and FL collected the data; MSM and JS analyzed the data; MSM and DK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Data availability statement

Data will be available via the Dryad Digital Repository.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109670>.

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