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Food production and biodiversity are not incompatible in temperate heterogeneous agricultural landscapes

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We need landscape-scale approaches to design and manage agro-ecosystems that can sustain both agricultural production and biodiversity conservation. In this study, yield figures provided by 299 farmers served to quantify the energy-equivalents of food production across different crops in 49 1-km^2 landscapes. Our results show that the relationship between bird diversity and food energy production depends on the proportion of farmland within the landscape, with a negative correlation observed in agriculture dominated landscapes (≥ 64–74% farmland). In contrast, neither typical farmland birds nor butterflies showed any significant relationship with total food energy production. We conclude that in European temperate regions consisting of small-scale, mixed farming systems (arable and livestock production), productivity and biodiversity conservation may not be purely antagonistic, particularly when (semi-)natural habitats make up a large fraction of the landscape (≥ 20%).

KEYWORDS

sustainable agriculture, birds, butterflies, farmland, landscape scale, conservation

1 Introduction

Global agriculture production has more than doubled in the last 50 years and demand for food and agricultural products is foreseen to further increase in the next decades (Tilman et al., 2011; Ritchie, 2022). Corollary, agricultural practices strongly intensified and natural areas have undergone continued conversion to farmland (FAO, 2017). Specifically, at the field scale, the increased use of agrochemicals (e.g., mineral fertilizers and pesticides), mechanisation, and the use of high-yielding crop varieties have increased productivity. While at landscape scale field sizes have increased over time, farms have specialized on few crops (or even monocultures), permanent grasslands have been converted to arable fields, fallow lands have disappeared and semi-natural habitats such as field boundaries and hedgerows have been destroyed (Tscharntke et al., 2005). These land-use changes, have reduced, not only the biodiversity of natural habitats and traditional low-intensity agroecosystems, but also the flora and fauna of intensively used agroecosystems (Tscharntke et al., 2005; Sutcliffe et al., 2015; Warren et al., 2021; Rigal et al., 2023). Ironically, biodiversity is an important component for a sustainable long-term food production, as it supports a wide range of ecosystem services such as soil fertility, natural pest control and pollination (Pywell et al., 2015; Orford et al., 2016; Dainese et al., 2019; Albrecht et al., 2020; Gaba et al., 2020). With the increasing awareness on the consequences of farmland biodiversity loss and, at the same time, the need to ensure food production, research on the agricultural productivity-biodiversity frontier has considerably increased in the last two decades, with the focus moving from local- to landscape-scale processes (Tscharntke et al., 2012; Batary et al., 2020; Scherber, 2022).

A trade-off between agricultural production and biodiversity at landscape scale has been repeatedly demonstrated in tropical regions, where agriculture activities generally have detrimental effects on species typical of natural, habitats such as pristine forests (Phalan et al., 2011; Macchi et al., 2020; Wenzel et al., 2024). In Europe however, agricultural landscapes have developed over centuries and typically hold species dependent upon open or semi-open landscapes and adapted to a given level of land-use intensity (Burgi et al., 2015; Van Swaay et al., 2019; Boch et al., 2020). In these temperate regions, negative relationships have been evidenced in intensively managed arable and livestock production systems (Dross et al., 2017, 2018). Although Europe is characterized by a wide range of farming systems, landscape-scale studies from mixed, small-scale production systems are still rare (Feniuk et al., 2019). So far, most studies have either focused on the extent of farmland, or on the per unit area productivity, ignoring possible interactions between the two (e.g., Dross et al., 2018). This is regrettable, as structurally complex agricultural landscapes favour spatial connectivity and provide additional resources for farmland species (Villemey et al., 2015; Grass et al., 2019). Even butterflies, which typically depend upon farmland habitats, show the highest overall diversity in landscapes with a combination of farmed and semi-natural areas (Ouin and Burel, 2002; Zingg et al., 2018). The same is valid for birds, as many species require different habitats and a diversity of resources to complete their life cycles (Vickery and Arlettaz, 2012; Teillard et al., 2014). Consequently, structurally complex farmlands may compensate for local high-intensity management, leading to the productivity-biodiversity relationship being dependent on the extent of farmland within the landscapes (Tscharntke et al., 2005).

In this study, we analysed the relationship between agricultural productivity, defined as food energy production, and bird and butterfly diversity in 49 temperate agricultural landscapes of 1 km^2 each. In order to compare agricultural yields across grasslands and different arable crops, food energy, was used as a common metric of production per unit area (Dross et al., 2018; Feniuk et al., 2019). Contrary to most other studies, which use reference yield data from regional or national agricultural statistics, we collected actual yield data from 299 farmers, thus capturing the spatial and temporal heterogeneity of agricultural yields (Butsic et al., 2020). Birds and butterflies were selected as model taxa because they have been proven to be good bioindicators of farmland biodiversity, influenced by changes in agricultural management and landscape composition (Zingg et al., 2018). In addition, typical farmland species of both taxa have shown a dramatic decline in the last few decades (Gregory et al., 2019; Van Swaay et al., 2019).

We expected the productivity-biodiversity relationships for birds and butterflies to be predominantly negative. Negative relationships have been repeatedly shown at the field scale, for example when comparing yield and biodiversity of organic and conventional farming systems (Gong et al., 2022), as well at the landscape scale where agricultural intensification is generally associated with the decline of bird and butterfly populations (Warren et al., 2021; Rigal et al., 2023). However, in landscapes with a higher degree of heterogeneity, we anticipated that the negative effect of locally highly productive agriculture could be mitigated by the presence of semi-natural areas (Persson et al., 2010; Botham et al., 2015; Batary et al., 2020; Redhead et al., 2020). Conversely, in landscapes dominated by farmland, we anticipated that an increase in agricultural production would have a stronger negative effect on the diversity and abundance of birds and butterflies (Ekroos et al., 2010; Dross et al., 2017; Zingg et al., 2018; Rigal et al., 2023). As land is limited and the demand for food rising, the conflict between agriculture and biodiversity conservation is likely to increase further and calls for more research on the topic (see also Grass et al., 2021).

2 Materials and methods

2.1 Study sites

The study was conducted on the Swiss lowland Plateau, the most important agricultural area and densely populated region of Switzerland (426 inhabitants per km^2). The Biodiversity Monitoring Switzerland (BDM) conducts repeated biodiversity surveys in 520 systematically distributed landscape grid cells of 1 × 1 km across Switzerland (BDM Coordination Office, 2014). For this study, 49 BDM landscapes located on the Swiss lowland Plateau (altitude ranging from 400 to 800 m), with less than 25 ha of water bodies and paved areas were selected (electronic Supplementary material S1). For each of the 49 landscape grid cells (hereafter called landscapes), digitized information on land use was provided by the Swiss cadastral survey in 2014. The supplied GIS polygon layers were controlled and completed where necessary, using satellite images in ArcGIS (Version 10.2.2). Crop cover maps were provided by the cantonal agricultural offices in 2014. Because such maps were not available for some regions (cantons of Aargau and Vaud), these landscapes (n = 16) were visited and crops were mapped in summer 2016.

The study landscapes had on average (mean ± SD) 68 ± 16 hectares of farmland (ranging from 27 to 94 hectares) and were characterised by relatively small agricultural fields (mean field size was 1.32 ± 1.68 hectares). Farmers cultivated in total 12 different crop categories, with cereals, intensively managed grasslands and silage maize being the most abundant ones in terms of area cultivated (Figure 1). The landscapes showed a high level of crop diversity, visually represented in Figure 2. On average, there were 7.4 crops (± 2) present in each landscape, and the crop diversity, measured using the Shannon index based on the total area per crop category, was 1.34 (± 0.4).

2.2 Biodiversity

Data on species richness and abundance of birds and butterflies were provided by the Swiss Biodiversity Monitoring and the Monitoring of common breeding birds. Repeated transect counts (seven times per sampling year for butterflies and three times for birds, conducted between April and September) were used to assess species presence in the landscapes. Surveys were conducted along transects of 2.5 km (BDM Coordination Office, 2014). For data analysis, birds and butterflies were classified into two groups: (1) all species pooled within the corresponding taxonomic group; and (2) typical farmland species. Complete species lists can be found in the

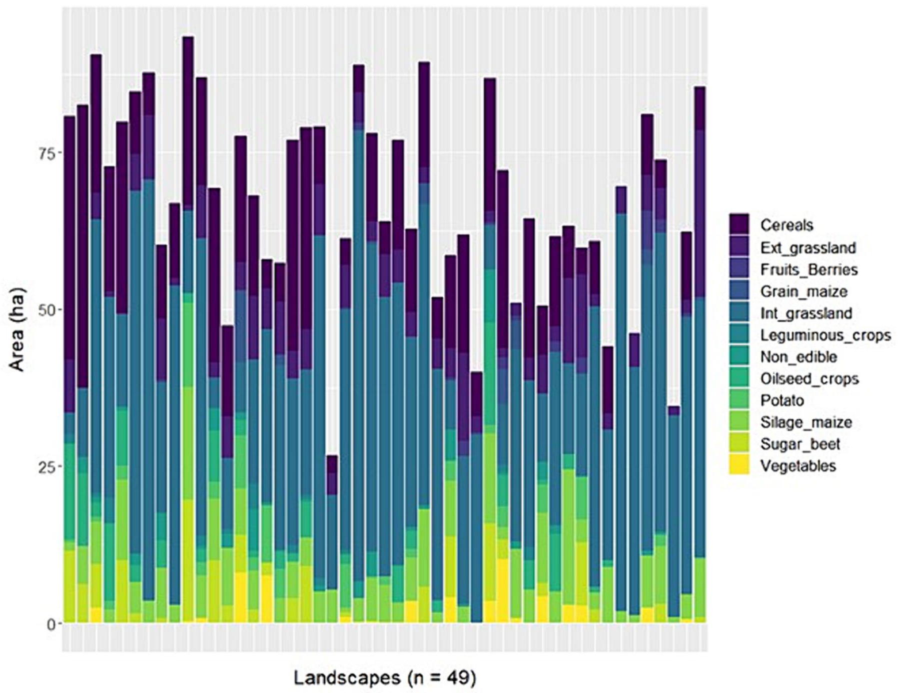

FIGURE 1
Composition of the 49 study landscapes showing the proportions (ha) of the different agricultural crops grouped in twelve categories. The non-farmed habitats (grey) consisted mainly of forests (mean ± SD = 15 ± 13 ha), impervious (e.g., buildings and streets, 8 ± 6 ha) and non-farmed vegetated areas (e.g., gardens, 3 ± 7 ha), and to a lesser extent of waterbodies, hedges and unvegetated areas (e.g., gravel, rock, sand). Ext., extensively managed; Int., intensively managed.

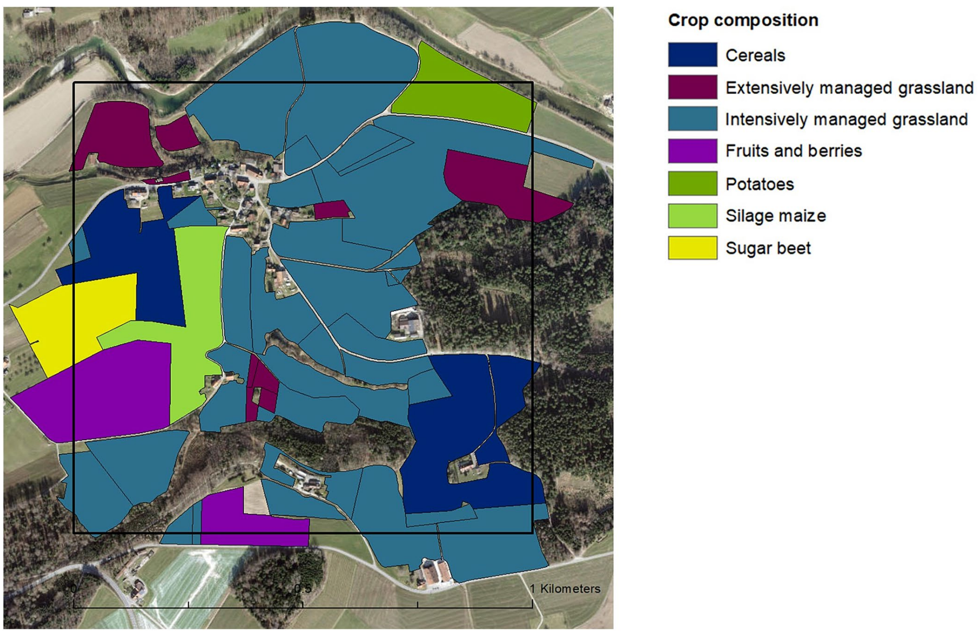

FIGURE 2
Example of a 1-km² study landscape showing the variegated spatial agriculture configuration with relatively small fields and high crop diversity.

Supplementary information (electronic Supplementary material S2). As total and farmland butterfly species richness and abundance were highly correlated (Pearson correlation coefficient > 0.9), results are only shown for total butterfly species richness and abundance.

2.3 Productivity

To estimate agricultural productivity, interviews with 299 farmers (in person or via questionnaires) were conducted. Farmers were asked to provide information on crop area, production system, yield (biomass), as well as the frequency of use (number of cuts and grazing events per year) for grasslands, over a three-year period (e.g., 2012–2014 or 2013–2015). Interviews led to a minimum of ten valid observations for yield and frequency of use per landscape.

2.3.1 Multiple imputation for missing yield values

Yield estimates were not available for all fields, either because farmers were not willing to participate in the survey (farmer participation ranged from 19 to 100% with an average of 68%, calculated as the percentage of agricultural area covered by the interview), or because yields were unknown (see electronic Supplementary material S3). Therefore, prior to the statistical analysis, we completed our yield dataset using Multiple Imputation (MI). As an advanced procedure for handling missing data, MI consists of estimating the missing data multiple times to create several complete versions of an incomplete dataset (van Buuren, 2012). We used predictive mean matching (PMM) from the R Package *mice* to impute the missing yield values and to create 50 completed datasets (van Buuren and Groothuis-Oudshoorn, 2011). The PMM procedure subsamples from the observed data and predicts the value of the target variable Y according to the specified imputation models:

i) Grassland yield = Grassland category + Frequency of use + Management + Year + Landscape + Region + Elevation
ii) Arable yield = Crop category + Management + Year + Landscape + Region + Elevation

The following predictors were included: grassland or crop category (the same as in Figure 1), the frequency of use for grasslands (number of cuts and grazing events per year), the management (organic, extensive or conventional) and the year (2012 to 2015). In addition, landscape (ID), elevation (meter above sea level), and the region (Swiss canton) were included. Because MI can generate implausible values (e.g., 200 dt/ha for wheat), we restricted the yield values after the imputation (post-processing), to the 1st and 3rd quartile of real yield values given by farmers. For more information on the missing yield values in general and the MI process see electronic Supplementary material S3.

2.3.2 Food energy-equivalent per landscape

For each of the 50 completed datasets, we calculated the mean crop yield per ha, averaging over all three sampling years and fields, within each landscape. Using this, we calculated the total food energy production *P* (in GJ of metabolizable energy *ME* per year), in each landscape for each imputed dataset *k* as follows:

$$P_{jk} = \sum_{i=1}^{n} X_{ijk}\ A_{ij}\ CF_i\ ME_i$$

Where, *j* refers to the study landscape and *i* to the crop category. *X* is the averaged crop yield (dt ha^{-1} $year^{-1}$) from the imputed dataset, *A* the crop area (ha) from the agricultural survey or crop mapping, *CF* the conversion factor, which accounts for the losses during food processing or conversion (see electronic Supplementary material S4) and *ME* the content of metabolizable energy per unit weight of edible portion (GJ dt^{-1}) from the Swiss Food Composition Database (FSVO, 2017). Non-edible crops, such as ornamental plants (e.g., Christmas trees), by-products such as straw, and landscape features such as wildflower strips, or hedgerows were attributed a food energy content of zero. In general, we accounted for one main crop per year (except on vegetable fields, where we accounted for two harvests per year), while catch crops covering the soil during winter were not included in the productivity estimates.

2.3.3 Crop-use scenarios

We calculated total food energy production per landscape for two scenarios. In scenario 1, we assumed that all crops would be converted in an edible form and directly consumed by humans, except for fodder crops (i.e., silage maize and grass) which were expressed as the energy-equivalent of edible meat (in GJ) produced per unit weight. In scenario 2 (a more realistic estimation of joules produced for human consumption), we accounted for the fact that some edible crops are also used as animal feed; in cereals, for example, a share of 42% is used as animal feed in Switzerland, mostly to produce meat (Bundesamt für Statistik, 2016). We included the two scenarios to consider the aspects of the feed/food debate and the influence this has on the ultimate human food production of agricultural landscapes (Mottet et al., 2017). Information on the use of the crops in the two scenarios and the energetic values of the products can be found in the electronic Supplementary material S4.

2.4 Statistical analysis

Species richness, abundance and Pielou's evenness index of birds and butterflies were used as response variables. While models were run on total and farmland species richness and abundances, Pielou's evenness was calculated for total birds and butterflies. Food energy production per landscape in gigajoule (GJ) and the amount of farmland in hectare (ha) were included as explanatory variables. We used the following generalized linear models (GLM) with Poisson (for species richness), negative binomial (for abundance) or Gaussian (for Pielou's evenness) distributions:

$$\text{Response variable} = \text{food energy} + \text{farmland} + \left(\text{food energy x farmland}\right)$$

The interaction was removed if not significant. The regression models were fitted to the n (= 50) imputed datasets and the model results were pooled using the R Package *mitools* (Lumley, 2015). Hereby, for logistic regression modelling in combination with MI, the pooled regression coefficients and standard errors were obtained by using Rubin's Rule (Rubin, 1976). The pooled coefficient was derived by averaging the regression coefficient estimates from each complete data analysis result across the imputed datasets. The standard error was obtained by pooling the variance between as well as within imputations, which account for sampling and imputation uncertainty, respectively (Eekhout et al., 2017). The variability between the imputations reflects the uncertainty of the actual value (van Buuren, 2012).

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Finally, in models where the interaction term between food energy production and proportion of farmland was significant, the threshold, i.e., when the trend changes sign due to the proportion of farmland in the landscape (or in other words when food energy production has no influence on the response variable) was computed using model outputs.

3 Results

Total food energy produced (given as metabolizable energy for human consumption) averaged to 2′344 GJ (± 1′958) per 1-km² landscape and year for scenario 1 (all food energy production directly consumed by humans) and 1′921 GJ (± 1′713) for scenario 2 (part of the production used as animal feed to produce meat, electronic Supplementary material S5). Computed per hectare of farmland, food energy production averaged to 33 GJ/ha (± 24) for scenario 1 and 27 GJ/ha (± 21) for scenario 2. These food energy figures provide a landscape-scale measure of agricultural production reflecting the proportion of the landscape that is farmed, the types of crops grown within the landscape and the in-field yield of those crops. In other words, at the landscape scale the proportion of farmland, the share of highly productive crops (such as sugar beet or potatoes) correlated with the total food energy produced (see electronic Supplementary material S5). Note that the food energy figures given by scenarios 1 and 2 were highly correlated ($r = 0.99$).

3.1 Relationship between biodiversity and food energy

Results showed a significant interaction effect between food energy production and the extent of farmland. The nature of the interaction indicates that the relationship between productivity and overall bird richness, abundance and evenness varies depending on the amount of farmland within the landscapes (Table 1). Hereby, overall bird species richness and abundance decreased with food energy production in landscapes with high shares of farmland (i.e., ≥ 74 or ≥ 72 ha respectively), but increased in landscapes with lesser fractions of farmland (Figure 3). The same pattern was observed for total bird evenness, where the threshold at which the regression changed from positive to negative was at 64 ha of farmland per landscape. Farmland birds were analysed separately as a subgroup, however no significant effects on species richness or abundance were detected (Table 1). Further analyses revealed that although some farmland bird species such as the Eurasian Skylark (*Alauda arvensis*) responded positively to food energy production, most species had a neutral or slightly negative response (electronic Supplementary material S7).

No significant relationship between butterfly diversity or abundance, and food energy production at landscape scale was found (electronic Supplementary material S6). Single species analyses confirmed that most farmland butterflies responded neutrally to food energy production with four exceptions; namely the Ringlet (*Aphantopus hyperantus*) the Queen of Spain Fritillary (*Issoria lathonia*) and the Large Skipper (*Ochlodes sylvanus*) that significantly decreased with food energy production, and the Essex skipper (*Thymelicus lineola*) that significantly increased with food energy production.

4 Discussion

So far agricultural productivity-biodiversity studies were mostly conducted at field scale. The novelty of the present study lies in the fact that it was conducted at the landscape scale (1 × 1 km plots, equivalent to 100 ha) and was based on real yield information. Contrary to our expectations, observed relationships between total food energy produced and biodiversity per landscape were not predominantly negative, indicating that in intensively managed but small-scale mixed farmland, food production and biodiversity conservation are not necessarily incompatible.

In our studied Swiss lowland landscapes, mean productivity (food energy production) averaged to 33 GJ/ha (± 24) for scenario 1 and 27 GJ/ha (± 21) for scenario 2. In comparison with other European studies, it represents intermediate agricultural systems, accounting neither for the very low-yield extensively managed grassland-based systems (as found in Poland, Feniuk et al., 2019) nor for the very high-productivity, industrialized, monocultural systems (as found in France, Dross et al., 2017). Thus, unsurprisingly, farmland sensitive species adapted to very low-productivity systems are absent from our datasets. Such species, like the corn crake (*Crex crex*) and the woodchat shrike (*Lanius senator*), gradually vanished from the Swiss lowland decades ago (Keller et al., 2010). The range of productivity levels in our study system is also limited: all our study sites contained at least 27% of farmland (as shown in Figure 1). Subsequently we do not discuss our results in the light of the land sparing-sharing model, because this would require data on the density of wild species across a range of agricultural yields, including 100% unfarmed, or natural landscapes (Phalan, 2018). Therefore, we emphasize that conclusions drawn from this study are mostly valid in currently farmed European temperate regions with intermediate agricultural productivity and similar agri-environmental policies as implemented in Switzerland (see related paragraph in the next subsection).

4.1 Relationship between biodiversity and food energy

While the aspects of agricultural productivity and the extent of farmland are in general separately analysed (Jeliazkov et al., 2016; Dross et al., 2017), we show here that there exists a significant interaction between these two aspects. In landscapes characterized by a high proportion of farmland (≥ 64–74%), we observed a negative relationship between overall bird richness, abundance, evenness, and food energy production. This can be attributed to the limited availability of habitat elements (e.g., nesting sites) in cleared, agriculture-dominated landscapes (Tscharntke et al., 2012; Batary et al., 2020). Moreover, when agricultural areas are intensively managed, the depletion of food resources (e.g., invertebrates) exacerbates the negative impact on bird biodiversity (Vickery and Arlettaz, 2012; Rigal et al., 2023).

Conversely, we found that an increase in food energy production positively correlated with bird biodiversity in landscapes with lower proportions of farmland (≤ 64–74%). This suggests that the replacement of some low-energy yield with high-energy yield crop types, or the transitioning from grassland-dominated landscapes to mixed grassland and cereal landscapes, can enhance habitat heterogeneity and resource availability for

TABLE 1 Summary of the models showing the relationships between birds and butterflies and agricultural productivity given as total food energy produced.

Response	Intercept			Food energy (GJ)			Farmland (ha)			Food energy (GJ) x Farmland (ha)		
	Est.	Lower	Upper	Est.	Lower	Upper	Est.	Lower	Upper	Est.	Lower	Upper
Total bird SP	3.74	3.48	4.00	**2.31 * 10^{-4}**	**7.04 * 10^{-5}**	**3.93 * 10^{-4}**	− 1.05 * 10^{-3}	− 4.93 * 10^{-3}	2.84 * 10^{-3}	**−3.10 * 10^{-6}**	**−5.13 * 10^{-6}**	**−1.06 * 10^{-6}**
Total bird AB	6.40	5.94	6.87	**3.85 * 10^{-4}**	**9.84 * 10^{-5}**	**6.71 * 10^{-4}**	− 1.03 * 10^{-2}	− 1.71 * 10^{-2}	− 3.39 * 10^{-3}	**−5.33 * 10^{-6}**	**−8.86 * 10^{-6}**	**−1.81 * 10^{-6}**
Farmland bird SP	1.78	1.32	2.24	− 9.34 * 10^{-6}	− 7.28 * 10^{-5}	5.41 * 10^{-5}	5.24 * 10^{-3}	− 1.91 * 10^{-3}	1.24 * 10^{-2}			
Farmland bird AB	3.44	2.98	3.90	1.69 * 10^{-5}	− 4.85 * 10^{-5}	8.23 * 10^{-5}	5.25 * 10^{-3}	− 1.97 * 10^{-3}	1.25 * 10^{-2}			
Total bird EV	0.77	0.71	0.83	**2.92 * 10^{-5}**	**−7.06 * 10^{-6}**	**6.54 * 10^{-5}**	**1.31 * 10^{-3}**	**4.29 * 10^{-4}**	**2.19 * 10^{-3}**	**−4.51 * 10^{-7}**	**−8.95 * 10^{-7}**	**−6.07 * 10^{-9}**
Total butterfly SP	3.39	3.13	3.65	− 8.39 * 10^{-7}	− 4.05 * 10^{-5}	3.88 * 10^{-5}	− 3.44 * 10^{-3}	− 7.65 * 10^{-3}	7.62 * 10^{-4}			
Total butterfly AB	6.10	5.38	6.83	1.99 * 10^{-5}	− 8.54 * 10^{-5}	1.25 * 10^{-4}	− 5.48 * 10^{-4}	− 1.20 * 10^{-2}	1.09 * 10^{-2}			
Total butterfly EV	0.72	0.59	0.85	− 2.29 * 10^{-6}	− 2.16 * 10^{-5}	1.70 * 10^{-5}	− 3.14 * 10^{-4}	− 2.42 * 10^{-3}	1.79 * 10^{-3}			

Results are based on the pooled model outcomes from the 50 imputed datasets for scenario 2 (model results for scenario 1 can be found in the electronic Supplementary material S6). For each model, the estimates, including confidence intervals, are given on log scale for SP and AB and original scale for evenness. Significant effects are shown in bold. AB, abundance; EV, Evenness; SP, species richness; GJ, gigajoule; ha, hectare.

birds on farmland. In landscapes with lower shares of farmland, the presence of other semi-natural or man-made habitats, such as forests, hedges, or settlements, further contributes to habitat complexity. These structurally diverse landscapes not only promote local diversity in agroecosystems, particularly for mobile organisms (Zingg et al., 2018; Redhead et al., 2020; Kühne et al., 2022), but also potentially offset the negative effects of within field high-intensity management practices (Tscharntke et al., 2005; Batary et al., 2020).

The depicted relationships between bird evenness and food energy production indicate changes in species dominance when productivity increases, highlighting that there is no optimal land-use intensity and configuration that will maximize all species (Teillard et al., 2014).

We did not find a significant relationship between butterfly diversity or abundance, and food energy production at landscape scale. Neutral productivity relationships for butterflies were mostly described in tropical agroforestry systems, where crops such as vanilla, coffee or cacao are produced under shade trees in spatially combined and complex systems, which can provide both high yield and biodiversity (Clough et al., 2011; Wurz et al., 2022). In temperate agro-ecosystems, predominantly characterized by monocultures of grasslands and arable fields, productivity is maintained at high levels through agricultural inputs, which often reduce biodiversity (Kleijn et al., 2009; Gong et al., 2022). Nonetheless, in our system, several aspects may explain the observed neutral relationships between food energy production and butterfly biodiversity: (i) productivity in GJ does not equal agricultural intensity; (ii) current agroecological measures, including in as well as out of production agri-environment schemes, effectively maintain biodiversity; (iii) biodiversity supports productivity. The three points are described more in detail in the following paragraphs.

i) There is no doubt that agriculture has a strong influence on biodiversity. However, it is not agricultural productivity *per se*, but management practices (e.g., soil work, fertilizer and pesticide input), fields size, crop identity and crop diversity which mostly influence biodiversity (Kremen, 2015; Hass et al., 2018; Sirami et al., 2019). While in-field productivity strongly depends on management intensity (e.g., extensively vs. intensively managed grasslands, Kleijn et al., 2009; Boch et al., 2021), landscape productivity is strongly linked to the composition of the landscape. In our mixed agricultural landscapes, productivity increased with the share of farmland and of crops with high energetic values and high yields (i.e., sugar beets, potatoes and cereals, see electronic Supplementary material S5). Whereas high in-field productivity does imply high management intensity (e.g., higher cereal yield due to higher fertilizer and pesticide application), higher landscape-scale productivity cannot be directly linked to crop management practices.
ii) Agricultural policy in Switzerland follows the framework of environmental cross compliance (Aviron et al., 2009; Swiss Federal Council, 2013). Sustainable agricultural practices such as intercropping, crop rotations or reduced agrochemical use aim to reduce environmental impact and safeguard production. In addition, Swiss farmers have to dedicate at least 7% of their land to wildlife-friendly agri-environment schemes (at the time of the study, 13% of the Swiss lowland farmland was managed under such schemes). These schemes, which include, for

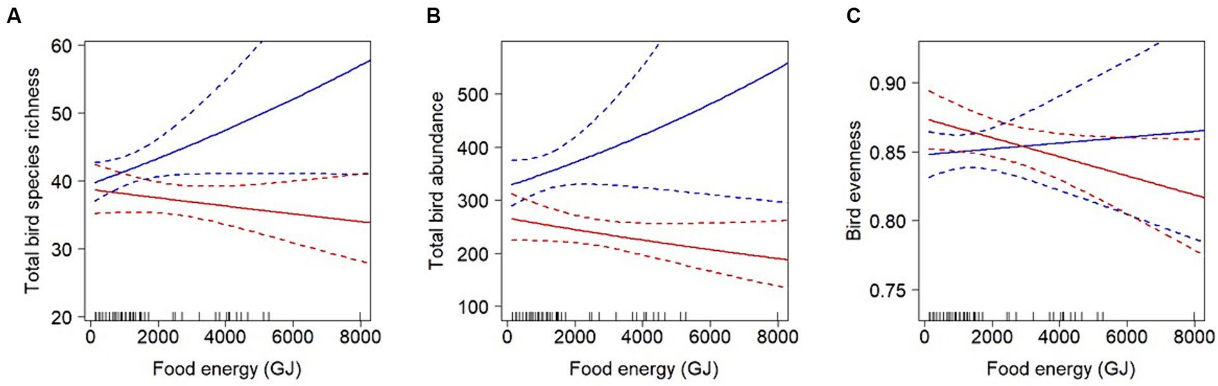

FIGURE 3
The relationship between bird species richness **(A)**, abundance **(B)**, evenness **(C)** and food energy-equivalents (given as metabolizable energy for human consumption, i.e., scenario 2) depends on the amount of farmland within the respective 1-km^2 landscape (see Table 1 for the parameters of the linear models). The figure shows the predicted regression lines for landscapes with 60 ha (blue) and 80 ha of farmland (red) that fall below or above, respectively, the threshold where the regression line changes slope. Threshold values are at 74, 72 and 64 ha of farmland for total bird species richness, abundance and evenness, respectively. Shown are pooled predictions with 95% confidence intervals from the (n = 50) models. The means of the imputed food energy values in gigajoule (GJ) are shown as tick marks at the bottom. Relationships with butterflies were not significant and can be found in the electronic Supplementary material S6.

example, extensively managed grasslands and wildflower strips, have been shown to promote farmland biodiversity, including butterflies, at local (Aviron et al., 2009; Bruppacher et al., 2016) and landscape scale (Zingg et al., 2019). Moreover, many farms in our study region still combine livestock and crop production, meaning that our landscapes all display a matrix combining grassland and arable fields (Figure 1). Although arable and grassland specialist species thrive in regions dominated by either production system, most species prefer mixed landscapes (Botham et al., 2015; Dross et al., 2018).

iii) It is intuitively assumed that the presence of natural or low-intensity managed areas promotes biodiversity at the cost of agricultural productivity because it excludes land from production and reduces local yield, respectively. However, there is more and more evidence of biodiversity-mediated benefits to agricultural production (Batary et al., 2020). For example, it was demonstrated in a UK field-scale study that wildlife-friendly habitats that promote pollinators and other beneficial organisms can increase yield per unit area, compensating for the land that was taken out of production (Pywell et al., 2015). Similarly, it has been shown that crop yield resilience is positively related to semi-natural habitats in the landscape (Redhead et al., 2020). At local scale, it has been known for a long time that phytomass production is higher and more stable in species-rich grasslands (Hautier et al., 2014). However, the reliance of modern agriculture on intensive management such as the prophylactic use of agrochemicals may mask (or even suppress) potential benefits from ecosystem services (Gagic et al., 2017), also in our system.

5 Conclusion

The main finding of this study is that in temperate mixed agricultural landscapes, high agricultural production, in terms of joules produced per 1-km^2 landscape (100 ha), is not necessarily incompatible with high biodiversity. While total bird species richness, abundance and diversity were negatively correlated with agricultural production in landscapes dominated by farmland, we found no relationship in landscapes with a share of ≥30–40% of non-farmed habitats. In addition, and more surprisingly, neither farmland birds, nor butterflies were correlated with total food energy production. Although it is not possible to establish any causality from our analyses, non-farmed areas such as forest patches and hedges (semi-natural habitats represented usually ≥20% of the studied landscapes), small fields (field size averaged 1.32 ha), wildlife-friendly agri-environment schemes and high crop diversity, seem to mitigate the negative influence of intensive and highly productive in-field management practices (Konvicka et al., 2016; Grass et al., 2019; Sirami et al., 2019; Zingg et al., 2019; Batary et al., 2020). In such small scale, well connected heterogeneous landscapes, the productivity-biodiversity trade-off may be less pronounced or absent. In conclusion, as the main purpose of agriculture is to produce food for human consumption, it is promising to see that there are ways to design multi-functional agro-ecosystems that support both biodiversity and agricultural food production (Batary et al., 2020; Finch et al., 2020).

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: https://doi.org/10.5061/dryad.hmgqnk9nf.

Author contributions

SZ: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. JG: Conceptualization, Methodology, Writing

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2024.1377369/full#supplementary-material

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Supplementary Material

For Zingg et al., 2024. Food production and biodiversity are not incompatible in temperate heterogeneous agricultural landscapes. *Frontiers in Sustainable Food Systems*.

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S1 – Study region

S2 – Bird and butterfly occurrence

S3 – Multiple imputation of missing yield values

S4 – Estimation of food energy produced

S5 – Total food energy produced at landscape scale

S6 – Additional results for crop-use scenarios and butterflies

S7 – Single species analyses

S1 - Study region

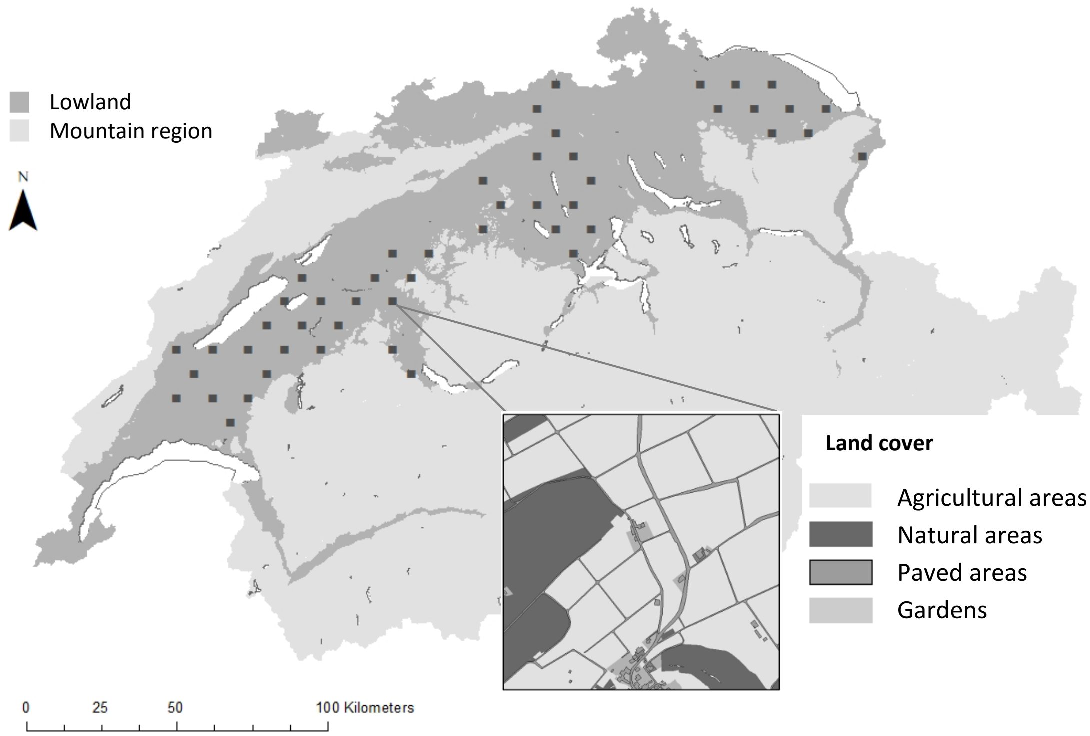

Figure S1.1. Map of Switzerland with the selected 1 x 1 km landscapes in this study (n = 49). The insert shows the detailed configuration of one landscape as an example.

S2 – Bird and butterfly occurrence

In the 49 study landscapes, a total of 99 bird species were recorded. Per landscape, on average 40 ± 7.5 (± SD) bird species were detected, including 8 (± 1.5) farmland species. Bird abundance (i.e. number of breeding pairs per landscape) was, on average, 307 (± 119.2), ranging from 93 to 580. Farmland bird abundance ranged from 14 to 88, with a mean of 46 (± 16.9). In total 60 butterfly species were detected, on average 23 (± 5.9) species and 448 (± 263.3) individuals were observed per landscape (range 113–1123).

Table S2.1. The table below shows the minimal and maximal abundance per landscape and the number of landscape squares (Nlan), out of 49, in which a given species was observed. Information on habitat (farmland vs non-farmland) was obtained from the Swiss Ornithological Institute for birds and from Benz et al. (1987) for butterflies. Red List status were retrieved from Keller et al. (2010) and Wermeille et al. (2014) for birds and butterflies respectively. Abbreviations: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, NA = not available.

Taxa	Latin name	Farm land	Red list	Min. abund.	Mean abund.	Max. abund.	N_{lan}
Bird	*Accipiter gentilis*	No	LC	1	1	1	1
Bird	*Accipiter nisus*	No	LC	1	1	1	4
Bird	*Acrocephalus palustris*	No	LC	1	4	8	7
Bird	*Acrocephalus scirpaceus*	No	LC	1	11	25	7
Bird	*Aegithalos caudatus*	No	LC	1	1	3	16
Bird	*Alauda arvensis*	Yes	NT	1	8	35	21
Bird	*Alcedo atthis*	No	VU	1	1	2	3
Bird	*Anas platyrhynchos*	No	LC	1	3	14	29
Bird	*Anser anser*	No	NA	1	1	1	1
Bird	*Apus apus*	No	NT	1	3	7	15
Bird	*Apus melba*	No	NT	30	30	30	1
Bird	*Asio otus*	Yes	NT	1	1	1	1
Bird	*Buteo buteo*	Yes	LC	1	2	4	45
Bird	*Carduelis cannabina*	Yes	NT	1	3	8	7
Bird	*Carduelis carduelis*	No	LC	1	4	13	36
Bird	*Carduelis chloris*	No	LC	1	7	44	46
Bird	*Certhia brachydactyla*	No	LC	1	5	12	35
Bird	*Certhia familiaris*	No	LC	1	3	10	14
Bird	*Ciconia ciconia*	Yes	VU	1	1	1	2
Bird	*Cinclus cinclus*	No	LC	1	1	2	7
Bird	*Coccothraustes coccothraustes*	No	LC	1	2	4	11
Bird	*Columba livia domestica*	No	NA	1	2	5	5
Bird	*Columba oenas*	No	LC	1	1	3	9
Bird	*Columba palumbus*	No	LC	1	7	22	48
Bird	*Corvus corax*	No	LC	1	1	1	12
Bird	*Corvus corone*	Yes	LC	1	7	18	49
Bird	*Corvus monedula*	Yes	VU	6	6	6	1
Bird	*Coturnix coturnix*	Yes	LC	1	2	3	3
Bird	*Cuculus canorus*	No	NT	1	1	4	15

Taxa	Latin name	Farm land	Red list	Min. abund.	Mean abund.	Max. abund.	N_{lan}
Bird	*Cygnus olor*	No	NA	1	2	3	2
Bird	*Delichon urbicum*	No	NT	1	11	48	20
Bird	*Dendrocopos major*	No	LC	1	4	8	41
Bird	*Dendrocopos minor*	No	LC	1	1	1	3
Bird	*Dryocopus martius*	No	LC	1	1	3	17
Bird	*Emberiza calandra*	Yes	VU	5	5	5	1
Bird	*Emberiza citrinella*	Yes	LC	1	6	13	39
Bird	*Emberiza schoeniclus*	No	VU	1	1	1	4
Bird	*Erithacus rubecula*	No	LC	1	10	31	42
Bird	*Falco subbuteo*	No	NT	1	1	1	5
Bird	*Falco tinnunculus*	Yes	NT	1	1	3	29
Bird	*Ficedula hypoleuca*	No	LC	1	2	9	14
Bird	*Fringilla coelebs*	No	LC	5	27	56	49
Bird	*Fulica atra*	No	LC	1	6	13	8
Bird	*Gallinula chloropus*	No	LC	1	1	2	5
Bird	*Garrulus glandarius*	No	LC	1	3	7	37
Bird	*Hippolais icterina*	No	VU	4	4	4	1
Bird	*Hirundo rustica*	Yes	LC	1	8	26	37
Bird	*Lanius collurio*	Yes	LC	1	2	3	7
Bird	*Larus michahellis*	No	LC	1	1	1	1
Bird	*Locustella luscinioides*	No	NT	2	2	2	1
Bird	*Loxia curvirostra*	No	LC	1	2	4	5
Bird	*Luscinia megarhynchos*	No	NT	1	2	4	3
Bird	*Milvus migrans*	No	LC	1	1	2	37
Bird	*Milvus milvus*	Yes	LC	1	1	3	40
Bird	*Motacilla alba*	No	LC	1	4	12	47
Bird	*Motacilla cinerea*	No	LC	1	1	2	7
Bird	*Motacilla flava*	Yes	NT	1	1	1	1
Bird	*Muscicapa striata*	No	LC	1	4	15	30
Bird	*Oriolus oriolus*	No	LC	1	3	9	6
Bird	*Parus ater*	No	LC	1	7	22	32
Bird	*Parus caeruleus*	No	LC	1	11	27	49
Bird	*Parus cristatus*	No	LC	1	2	7	14
Bird	*Parus major*	No	LC	1	17	36	49
Bird	*Parus palustris*	No	LC	1	3	11	40
Bird	*Passer domesticus*	No	LC	1	33	96	47
Bird	*Passer montanus*	Yes	LC	1	8	24	44
Bird	*Pernis apivorus*	No	NT	1	1	1	2
Bird	*Phasianus colchicus*	Yes	NA	2	2	2	1
Bird	*Phoenicurus ochruros*	No	LC	1	10	27	46
Bird	*Phoenicurus phoenicurus*	Yes	NT	1	1	1	2
Bird	*Phylloscopus collybita*	No	LC	1	10	32	43
Bird	*Phylloscopus sibilatrix*	No	VU	1	1	1	2
Bird	*Phylloscopus trochilus*	No	VU	1	2	4	2
Bird	*Pica pica*	No	LC	1	3	9	41

Taxa	Latin name	Farm land	Red list	Min. abund.	Mean abund.	Max. abund.	N_{lan}
Bird	*Picus canus*	No	VU	1	1	1	1
Bird	*Picus viridis*	No	LC	1	1	3	27
Bird	*Podiceps cristatus*	No	LC	1	2	4	3
Bird	*Prunella modularis*	No	LC	1	3	13	20
Bird	*Pyrrhula pyrrhula*	No	LC	1	1	1	5
Bird	*Rallus aquaticus*	No	LC	1	1	1	1
Bird	*Regulus ignicapilla*	No	LC	1	8	28	40
Bird	*Regulus regulus*	No	LC	1	5	24	30
Bird	*Saxicola rubicola*	Yes	NT	1	2	2	5
Bird	*Serinus serinus*	No	LC	1	4	11	27
Bird	*Sitta europaea*	No	LC	1	5	12	44
Bird	*Streptopelia decaocto*	No	LC	1	2	7	16
Bird	*Streptopelia turtur*	Yes	NT	1	1	1	1
Bird	*Strix aluco*	No	LC	1	1	1	3
Bird	*Sturnus vulgaris*	Yes	LC	1	11	29	48
Bird	*Sylvia atricapilla*	No	LC	1	25	71	48
Bird	*Sylvia borin*	No	NT	1	3	12	24
Bird	*Sylvia communis*	Yes	NT	1	2	2	2
Bird	*Tachybaptus ruficollis*	No	VU	1	3	4	3
Bird	*Troglodytes troglodytes*	No	LC	1	11	39	43
Bird	*Turdus merula*	No	LC	2	25	88	48
Bird	*Turdus philomelos*	No	LC	1	7	25	40
Bird	*Turdus pilaris*	Yes	VU	1	4	12	22
Bird	*Turdus viscivorus*	No	LC	1	3	8	30
Bird	*Vanellus vanellus*	Yes	CR	2	2	2	1
Butterfly	*Aglais urticae*	Yes	LC	1	10	74	43
Butterfly	*Anthocharis cardamines*	Yes	LC	1	4	15	21
Butterfly	*Apatura iris*	No	NT	1	1	2	4
Butterfly	*Aphantopus hyperantus*	Yes	LC	2	32	222	41
Butterfly	*Aporia crataegi*	Yes	NT	3	3	3	1
Butterfly	*Araschnia levana*	No	LC	1	8	35	23
Butterfly	*Argynnis adippe*	Yes	LC	1	1	1	1
Butterfly	*Argynnis paphia*	No	LC	1	4	23	21
Butterfly	*Aricia agestis-Komplex*	No	LC	1	2	6	14
Butterfly	*Boloria dia*	Yes	NT	1	3	7	4
Butterfly	*Brenthis daphne*	No	LC	1	2	5	6
Butterfly	*Brenthis ino*	No	NT	1	1	1	1
Butterfly	*Brintesia circe*	Yes	NT	1	1	1	1
Butterfly	*Carcharodus alceae*	Yes	NT	1	3	16	18
Butterfly	*Carterocephalus palaemon*	Yes	LC	1	1	1	1
Butterfly	*Celastrina argiolus*	No	LC	1	3	12	14
Butterfly	*Coenonympha pamphilus*	Yes	LC	1	21	79	47
Butterfly	*Colias croceus*	Yes	LC	1	10	47	30
Butterfly	*Colias hyale-Komplex*	No	LC	1	13	130	42
Butterfly	*Cupido alcetas*	Yes	NT	1	5	12	13
Butterfly	*Cupido argiades*	Yes	NT	1	10	48	27

Taxa	Latin name	Farm land	Red list	Min. abund.	Mean abund.	Max. abund.	N_{lan}
Butterfly	*Cupido minimus*	Yes	LC	1	1	1	1
Butterfly	*Erynnis tages*	Yes	LC	1	8	35	6
Butterfly	*Gonepteryx rhamni*	No	LC	1	3	13	29
Butterfly	*Inachis io*	No	LC	1	3	11	35
Butterfly	*Issoria lathonia*	Yes	LC	1	3	9	12
Butterfly	*Lasiommata maera*	Yes	LC	1	1	1	1
Butterfly	*Lasiommata megera*	Yes	LC	1	6	36	39
Butterfly	*Leptidea sinapis-Komplex*	Yes	LC	1	7	39	17
Butterfly	*Limenitis camilla*	No	LC	1	5	20	11
Butterfly	*Lycaena phlaeas*	Yes	LC	1	3	18	16
Butterfly	*Lycaena tityrus*	Yes	LC	1	2	2	6
Butterfly	*Maniola jurtina*	Yes	LC	1	87	550	39
Butterfly	*Melanargia galathea*	Yes	LC	1	20	103	32
Butterfly	*Melitaea athalia*	Yes	LC	1	2	2	2
Butterfly	*Melitaea diamina*	Yes	NT	1	1	1	1
Butterfly	*Melitaea parthenoides*	Yes	VU	9	9	9	1
Butterfly	*Ochlodes venata*	Yes	LC	1	6	42	32
Butterfly	*Papilio machaon*	Yes	LC	1	3	15	35
Butterfly	*Pararge aegeria*	No	LC	1	14	64	39
Butterfly	*Pieris brassicae*	Yes	LC	1	6	23	45
Butterfly	*Pieris mannii*	Yes	NT	8	20	43	3
Butterfly	*Pieris napi-Komplex*	No	LC	4	83	328	49
Butterfly	*Pieris rapae-Komplex*	No	LC	4	80	296	49
Butterfly	*Plebeius argus*	Yes	NT	1	1	1	1
Butterfly	*Polygonia c-album*	No	LC	1	4	12	28
Butterfly	*Polyommatus bellargus*	Yes	LC	2	2	2	2
Butterfly	*Polyommatus icarus*	Yes	LC	1	29	132	48
Butterfly	*Polyommatus semiargus*	Yes	LC	1	10	50	37
Butterfly	*Polyommatus thersites*	Yes	VU	1	1	1	1
Butterfly	*Pyrgus alveus-Komplex*	No	LC	1	2	4	3
Butterfly	*Pyrgus armoricanus*	No	NT	1	1	1	1
Butterfly	*Pyrgus malvae-Komplex*	Yes	LC	1	1	2	7
Butterfly	*Satyrium w-album*	No	LC	1	2	2	2
Butterfly	*Thecla betulae*	No	LC	1	1	1	4
Butterfly	*Thymelicus lineola*	Yes	LC	1	31	223	16
Butterfly	*Thymelicus sylvestris*	Yes	LC	2	10	26	12
Butterfly	*Vanessa atalanta*	Yes	LC	1	6	29	47
Butterfly	*Vanessa cardui*	Yes	LC	1	5	19	44
Butterfly	*Zygaena filipendulae*	Yes	LC	1	28	160	23

References

Benz, E., & Ligue suisse pour la protection de la nature. (1987). Tagfalter und ihre Lebensräume: Arten, Gefährdung, Schutz. Schweizerischer Bund für Naturschutz.

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Wermeille, E., Chittaro, Y., & Gonseth, Y. (2014). Rote Liste Tagfalter und Widderchen. Gefährdete Arten der Schweiz, Stand 2012. Bundesamt für Umwelt, Bern; Schweizer Zentrum für die Kartografie der Fauna, Neuenburg. Umwelt-Vollzug, 97.

S3 – Multiple Imputation of missing yield values

Unfortunately, yield estimates were not available for all fields, either because farmers were not willing to participate in the survey, or because yields were unknown (Fig. S3.1). The later happened typically when the crop's harvest was directly used on the farm as animal fodder (farmer participation ranged from 19% to 100% with an average of 68%). Therefore, yield data were completed using Multiple Imputation (MI; van Buuren, 2011). As an advanced procedure for handling missing data, MI consists of estimating the missing data multiple times to create several complete versions of an incomplete dataset. While 10–20 iterations is considered sufficient under moderate missingness (10–15%), we used 50 iterations to reach model convergence (visually checked as recommended in van Buuren, 2011). Because MI can generate implausible values, the yield values were additionally processed after the imputation to increase credibility; they were i) squeezed into the range of 1st and 3rd quartile yields reported by the farmers, and ii) vegetable yields were doubled (to account for multiple harvests per season). Though, MI are unbiased when missing values are missing at random which is believed to be the case here (Onkelinx et al., 2017). Figure S3.2 shows the raw data from farmer interviews (a) and the post-processed imputed yield values (b).

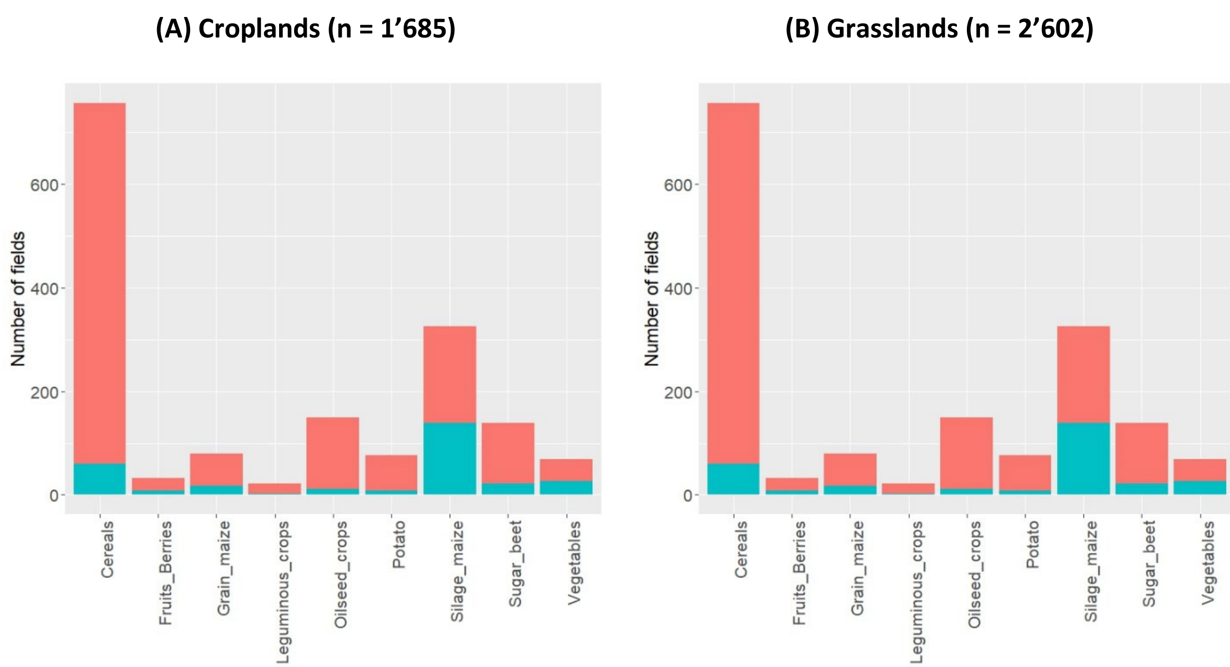


Figure. S3.1. Number of fields with known (Indian red) and unknown (turquoise) yield values for croplands (A) and grasslands (B). For grasslands, in cases when the exact yield of the grassland was unknown but the annual number of harvests was known, the later was included to estimate the yield.

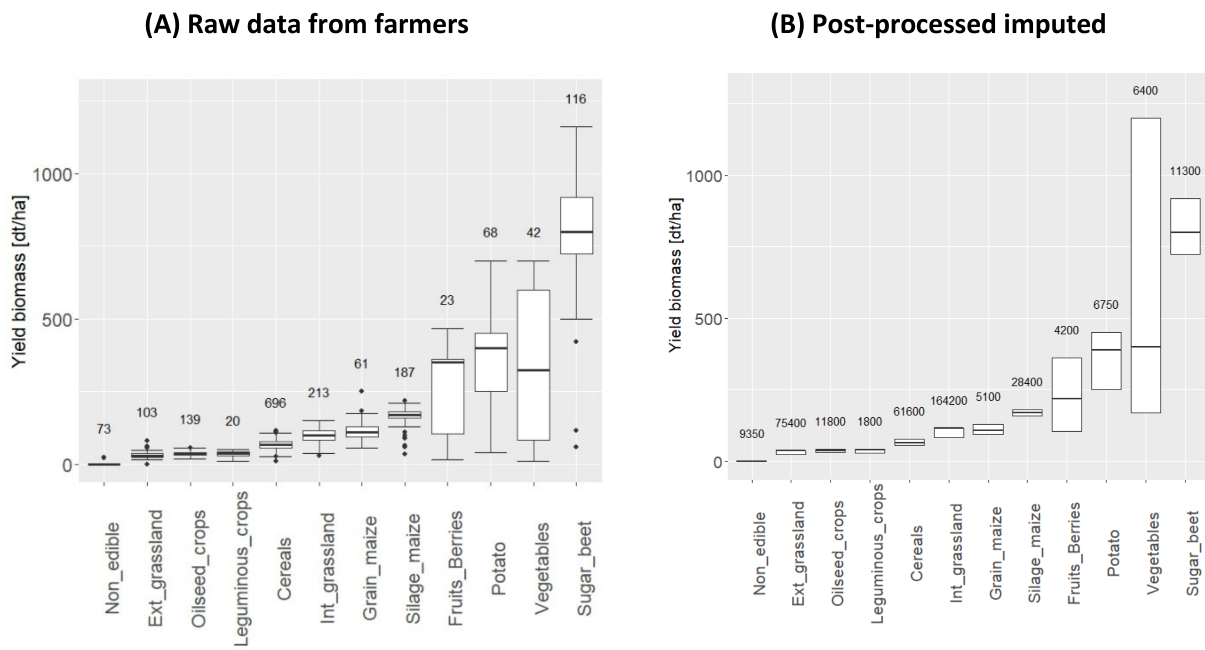


Figure. S3.2. Yield values before (A) and after multiple imputation (B). Shown are the medians, quartiles, outliers and the number of observations (above the bars). Grassland and silage maize yields are given in dry matter (DM), all others in fresh matter (FM). The summary statistics of the post-processed imputed yield values can be found in Table S3.1.

Table S3.1. Summary statistics of raw (before) and post-processed imputed yield values (dt/ha) of all crop types. Shown are the means and the standard deviation (SD) from the 50 imputed datasets. Abbreviations: Ext. = extensively managed, Int. = intensively managed.

	Raw data from farmers				**Post-processed imputed**			
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Sugar beet	809	177	60	1160	807	84	724	918
Vegetables	330	232	12	700	612	461	170	1200
Potato	372	141	40	700	356	92	250	452
Fruits and berries	251	156	18	467	238	122	106	363
Silage maize	167	25	35	220	170	10	160	180
Grain maize	119	35	58	250	111	16	95	130
Int. grassland	98	25	30	150	101	16	83	115
Cereals	68	15	12	115	67	9	58	78
Leguminous crops	37	10	10	52	37	6	30	44
Oilseed crops	37	7	18	58	37	5	32	42
Ext. grassland	33	13	0	82	32	6	25	38
Non-edible	3	8	0	25	0	0	0	0

References

Onkelinx, T., Devos, K., and Quataert, P. (2017). Working with population totals in the presence of missing data comparing imputation methods in terms of bias and precision. Journal of Ornithology 158, 603-615.

Van Buuren, S., & Groothuis-Oudshoorn, K. (2011). mice: Multivariate imputation by chained equations in R. Journal of statistical software, 45, 1-67.

S4 – Estimation of food energy produced

Table S4.1. Food energy content of edible portions per crop. The most common crop was used as reference for each crop category (e.g. wheat for cereals). The conversion factor (CF) determines the part of the agricultural product that is edible or retained during food processing (e.g. sugar extraction). Abbreviations: GJ = gigajoule, ME = metabolizable energy, DM = dry matter, FM = fresh matter, CF = conversion factor, 🐄= used as cattle fodder to produce beef, 🧍= used for human consumption, * edible by-product used as cattle fodder.

Crops	Food/fodder	CF	Food conversion	ME GJ t^{-1} edible portion [1]	ME GJ t^{-1} FM [2]	Scenario 1	Scenario 2
Cereals: wheat, barley, oat, rye, sorghum, spelt and triticale	Wheat grains	0.780	edible portion [3]	13.70	10.69	100% 🧍	58% 🧍
	Wheat grains	0.094	conv. to meat [6]	5.64	0.53		42% 🐄
Fruits and berries: berries, fruit orchards	Apple, raw	0.750	edible portion [3]	2.32	1.74	100% 🧍	100% 🧍
Oilseed crops: rapeseed, soja, sunflower	Rapeseed oil	0.370	oil extraction [4]	33.30	12.32	100% 🧍	100% 🧍
	Rapeseed cake*	0.087	conv. to meat [6]	5.64	0.49	63% 🐄	63% 🐄
Potato	Potato peeled, raw	0.900	edible portion [3]	3.20	2.88	100% 🧍	100% 🧍
Sugar beet: sugar and fooder beet	Sugar, white	0.180	sugar extraction [5]	17.00	3.06	100% 🧍	100% 🧍
	Pressed pulp *	0.022	conv. to meat [6]	5.64	0.12	24% 🐄	24% 🐄
	Molasse*	0.076	conv. to meat [6]	5.64	0.43	4% 🐄	4% 🐄
Vegetables: indoor and outdoor	Carrot, raw	0.900	edible portion [3]	1.58	1.42	100% 🧍	100% 🧍
Grain maize	Sweet maize, raw	0.790	edible portion [3]	3.90	3.08	100% 🧍	
	Graine maize	0.096	conv. to meat [6]	5.64	0.54		100% 🐄
Silage maize	Silage maize	0.077	conv. to meat [6]	5.64	0.43	100% 🐄	100% 🐄
Leguminous crops: field bean, leguminous and protein pea	Green beans	0.900	edible portion [3]	1.29	1.16	100% 🧍	
	Pea seeds	0.088	conv. to meat [6]	5.64	0.50		100% 🐄
Ext. grasslands: meadows and pastures	Hay	0.043	conv. to meat [6]	5.64	0.24	100% 🐄	100% 🐄
Int. grasslands: meadows and pastures	Green, silage fodder	0.069	conv. to meat [6]	5.64	0.39	100% 🐄	100% 🐄

(1) Federal Food Safety and Veterinary Office FSVO (2017): Swiss food composition database.
(2) Given in kg DM for silage maize and grasslands.
(3) FAO (2011) Global food losses and food waste. Food and Agriculture Organization of the United Nations, Rome.
(4) Average oil content was obtained from swiss granum with numbers from SwissOlio (2016). Source: www.swiss granum.ch
(5) Average sugar content was obtained from the SVZ annual reports from the years 2014 - 2016. Source: www.svz-fsb.ch
(6) see Table S4.2.

The method to estimate the food energy produced per crop (GJ per ton) can significantly vary among studies. The estimation is strongly influenced by several fundamental assumptions, such as the selection of reference crops and respective nutritional values, conversion factors and the various end-uses. Therefore, direct comparisons of absolute food energy values across studies may be challenging due to these underlying differences.

Conversion from crop to meat

As crops and crop by-products are often used as livestock feed, we calculated the amount of edible meat (specifically beef) that could be produced with it. Swiss standards were used for the calculations; the values may change in systems where cattle fattening is either very intensive or very extensive. We assumed that a cow would gain on average 1.1 kg per day (intermediate fattening intensity), for which an average daily food energy input of 39 MJ NEm (net energy for meat production) is required (Agroscope 2013). Consecutively, within one year (365 days), a cow gains 401.5 kg and uses 14’235 MJ NEm to attain the slaughter weight of 466.5 kg (assuming 65 kg were the start weight of the calf). From this 466.5 kg animal only around 35% are consumed by humans (Agridea 2014). Non-used and uneatable parts such as bones, fibers or cuts are eliminated during processing. Given our assumptions 14’235 MJ NEm were used to produce 163.3 kg beef, which means that with 87.2 MJ NEm, 1 kg of beef can be produced.

Table S4.2. The table shows how much edible meat is produced with 1 kg of a given crop or crop by-product. NEm energetic values for ruminants were obtained from the Swiss feed database. The feed conversion factor equals the amount of edible meat (in kg) which is produced per unit weight of a given crop. A cow would for example need 11 kg leguminous crops or 23 kg hay from extensively managed meadows to obtain the energy needed to produce 1 kg beef. Abbreviations: NEm = net energy for meat production, MJ = megajoule, DM = dry matter, FM = fresh matter.

Crop category	**Cattle feed**	**NEm MJ**	**per kg**	**NEm MJ needed for 1 kg meat**	**Conversion factor**
Cereals	Wheat, whole grain	8.23	FM	87.2	0.094
Oilseed crops	Rapeseed cake	7.55	FM	87.2	0.087
Sugar beet	Pressed pulp, fresh	1.94	FM	87.2	0.022
	Molasses	6.60	FM	87.2	0.076
Grain maize	Maize, grains	8.34	FM	87.2	0.096
Silage maize	Silage maize	6.69	DM	87.2	0.077
Leguminous crops	Protein pea seeds	7.71	FM	87.2	0.088
Extensively managed grassland	Hay (1)	3.75	DM	87.2	0.043
Intensively managed grassland	Hay, green and silage fodder (2)	6.02	DM	87.2	0.069

(1) *Average energetic value for mixed grassland communities harvested at growth stages 6 - 7 (late use)*

(2) *Average energetic value for mixed grassland communities with raygras harvested at growth stages 1-5 (early use)*

References

Agridea. (2014). Direktvermarktung von Fleisch. Agridea Lindau.

Agroscope. (2013). Fütterungsempfehlungen für Wiederkäuer (Grünes Buch). Posieux.

Agroscope & University of Zürich. (2017). Feedbase. The Swiss feed database. Available online at https://www.feedbase.ch, checked on 7/27/2017.

S5 – Total food energy produced at landscape level

Relationship between total food energy produced and crop-use scenarios

We estimated the total value of produced joules for human consumption in landscapes of 1 km^2 for two different crop-use scenarios. For scenario 1 we assumed that all crops would be converted into an edible form and be directly consumed by humans (i.e. a more plant-based diet). However, to consider that a large share of arable crops is used as livestock feed, we also included a more realistic estimation of produced joules in scenario 2 (see assumptions in Table S4.1). More information on the so-called feed-food debate can be found in Mottet et *al.* 2017. Total food energy produced for both scenarios are hereafter shown in Fig. S5.1.

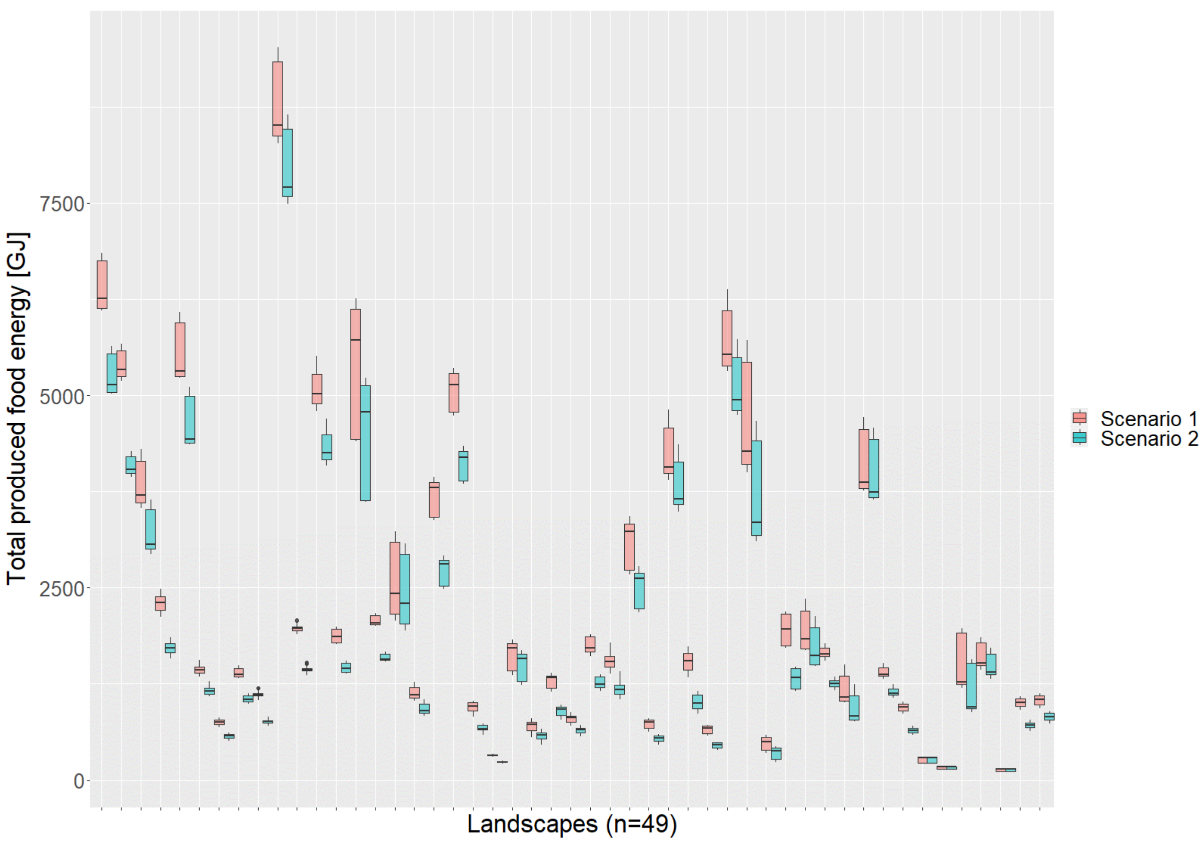


Figure. S5.1. Total food energy production (defined as metabolizable energy for human consumption in GJ per year) per landscape. Shown are the medians, quartiles and outliers from the 50 imputed datasets for all landscapes (n = 49) and both crop-use scenarios. Values for scenario 1 and 2 were highly correlated (R = 0.99).

Factors influencing total food energy produced at landscape level

The total food energy figures provide a landscape-scale measure of agricultural production reflecting: (a) the proportion of the landscape (1-km^2 study site) which is farmed and (b) the types of crops grown within the landscape. To describe the correlations between these factors and the total food energy produced (in GJ $year^{-1}$), linear models (Gaussian distribution) were fitted on the 50 imputed datasets.

Relationship between food energy production and area of farmland

As shown in figure S5.2, the area (or proportion as it corresponds to the number of ha out of 100) of farmland was positively correlated with the total food energy produced in scenario 1 (estimate = 61.9, CI = 30.0–93.8) and scenario 2 (estimate = 51.7, CI = 23.4–80.8).

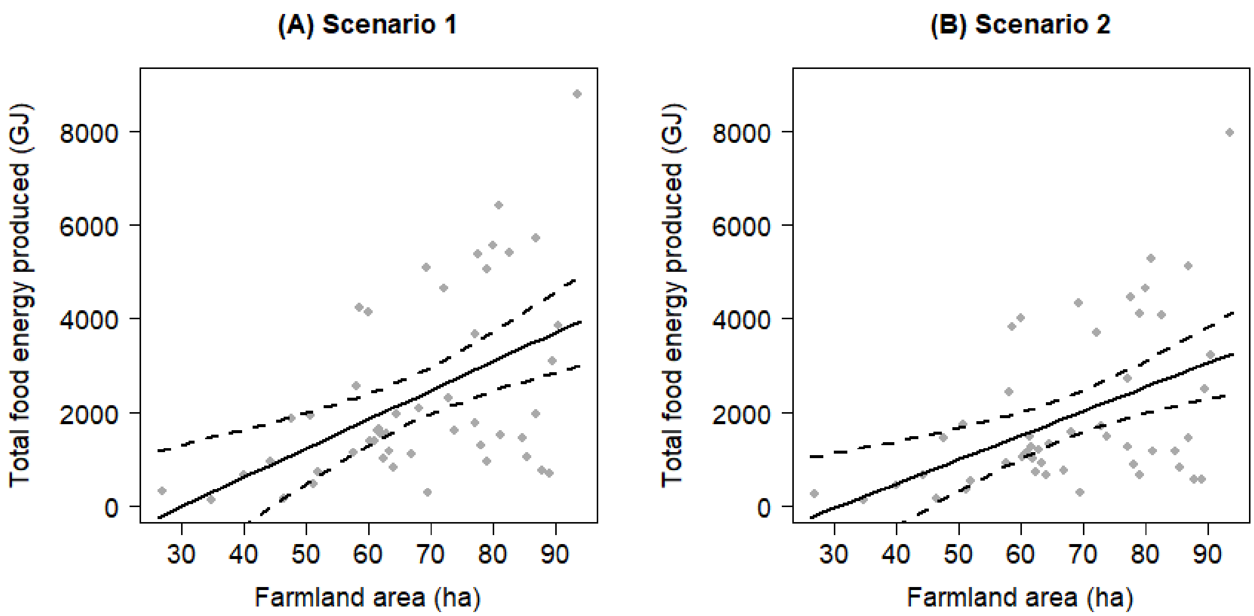


Figure. S5.2. The figure shows the relationships between the total food energy produced and the area of farmland within the landscapes for scenario 1 (A) and 2 (B). Shown are pooled predictions with 95% confidence intervals from the n (= 50) models. The means of the imputed food energy values are shown as dots.

Relationship between food energy production and crop types

The share of , sugar beet, potatoes, cereals, and oilseed crops in the landscape were positively correlated with the total food energy produced for both scenarios (Table S5.1).

Table S5.1. Summary of the models showing the relationships between the total food energy produced (in GJ) and the area of the different crops in the landscape (in ha). We only included crops that showed significant correlations in the univariate models. Results are based on the pooled model outcomes from the 50 imputed datasets. For each model, the estimates, including confidence intervals are given and significant effects are shown in bold. Abbreviations: GJ = gigajoule, ha = hectare and Int. = intensively managed.

	Food Energy (GJ)					
	Scenario 1			**Scenario 2**		
Crop type*	Est.	Lower	Upper	Est.	Lower	Upper
Intercept	-44.28	-305.66	217.11	-16.29	-231.68	199.09
Sugar beet	**249.99**	**209.63**	**290.35**	**251.88**	**214.05**	**289.72**
Potatoes	**119.49**	**78.00**	**160.98**	**115.83**	**78.85**	**152.80**
Cereals	**75.99**	**63.53**	**88.45**	**45.74**	**35.84**	**55.64**
Oilseed crops	**32.81**	**9.23**	**56.39**	**34.66**	**15.16**	**54.16**
Vegetables	**101.18**	**2.43**	**199.93**	89.65	-2.17	181.47
Int. grassland	4.71	-0.10	9.52	**4.49**	**0.48**	**8.50**
Silage maize	7.74	-8.14	23.61	6.12	-7.24	19.49

** In the univariate models, there was no significant effect of the area of grain maize, fruits and berries, extensively managed grasslands, leguminous and non-edible crops on the total produced food energy*

References

Mottet, A., de Haan, C., Falcucci, A., Tempio, G., Opio, C., & Gerber, P. (2017). Livestock: On our plates or eating at our table? A new analysis of the feed/food debate. Global Food Security, 14, 1-8.

S6 – Additional results for crop-use scenarios and butterflies

Relationship between biodiversity and productivity based on Scenario 1

The values for the total food energy production at landscape level (see Fig. S5.1) for the two crop-use scenarios were highly correlated (Pearson's correlation coefficient R = 0.99). The model results using food energy from scenario 2 are shown in the main text, the corresponding outcomes for scenario 1 are shown in the table below.

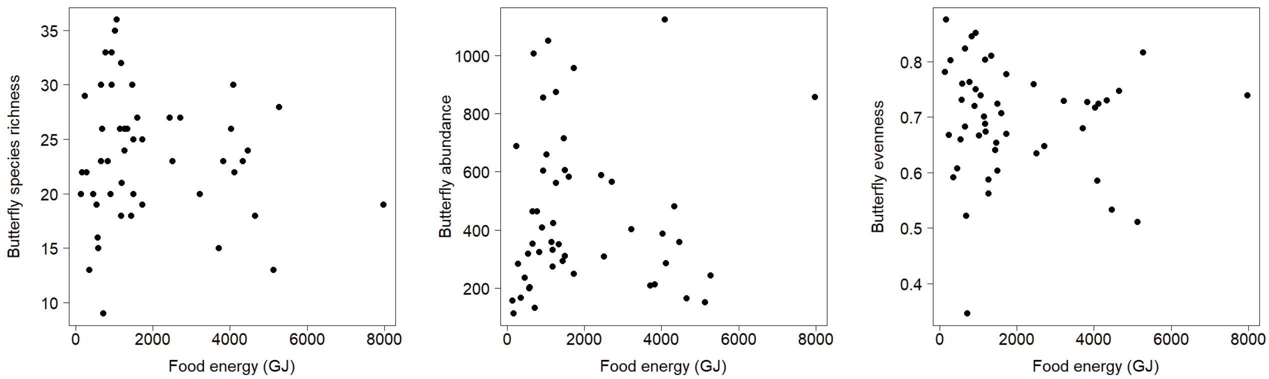
Table S6.1. Summary of the models showing the relationships between bird and butterfly abundance and species richness, and total produced food energy from scenario 1. Results are based on the pooled model outcomes from the 50 imputed datasets. For each model, the estimates, including confidence intervals, are given on a log scale for SP and AB and original scale for evenness. Significant effects are shown in bold. Abbreviations: AB = abundance, EV = evenness, SP = species richness, GJ = gigajoule, ha = hectare.

Response	**Intercept**			**Food energy (GJ)**			**Farmland (ha)**			**Food energy (GJ) x Farmland (ha)**		
	Est.	Lower	Upper	Est.	Lower	Upper	Est.	Lower	Upper	Est.	Lower	Upper
Total bird SP	3.73	3.46	4.00	**$1.97 * 10^{-4}$**	**$5.09 * 10^{-5}$**	**$3.43 * 10^{-4}$**	$- 9.52 * 10^{-4}$	$- 4.97 * 10^{-3}$	$3.06 * 10^{-3}$	**$- 2.63 * 10^{-6}$**	**$- 4.46 * 10^{-6}$**	**$- 7.97 * 10^{-7}$**
Total bird AB	6.39	5.90	6.87	**$3.28 * 10^{-4}$**	**$6.75 * 10^{-5}$**	**$5.88 * 10^{-4}$**	$- 9.94 * 10^{-3}$	$- 1.71 * 10^{-2}$	$- 2.76 * 10^{-3}$	**$- 4.57 * 10^{-6}$**	**$- 7.78 * 10^{-6}$**	**$- 1.36 * 10^{-6}$**
Farmland bird SP	1.78	1.32	2.24	$- 8.51 * 10^{-6}$	$- 6.47 * 10^{-5}$	$4.77 * 10^{-5}$	$5.29 * 10^{-3}$	$- 1.95 * 10^{-3}$	$1.25 * 10^{-2}$			
Farmland bird AB	3.44	2.98	3.89	$1.21 * 10^{-5}$	$- 4.60 * 10^{-5}$	$7.03 * 10^{-5}$	$5.37 * 10^{-3}$	$- 1.96 * 10^{-3}$	$1.27 * 10^{-2}$			
Total bird EV	0.81	0.76	0.85	$- 6.05 * 10^{-6}$	$- 1.24 * 10^{-5}$	$3.09 * 10^{-7}$	**$8.56 * 10^{-4}$**	**$6.66 * 10^{-5}$**	**$1.64 * 10^{-3}$**			
Total butterfly SP	3.40	3.14	3.66	$4.08 * 10^{-6}$	$- 3.11 * 10^{-5}$	$3.92 * 10^{-5}$	$- 3.74 * 10^{-3}$	$- 8.02 * 10^{-3}$	$5.41 * 10^{-4}$			
Total butterfly AB	6.13	5.41	6.85	$2.83 * 10^{-5}$	$- 6.51 * 10^{-5}$	$1.22 * 10^{-4}$	$- 1.35 * 10^{-3}$	$- 1.30 * 10^{-2}$	$1.03 * 10^{-2}$			
Total butterfly EV	0.72	0.59	0.85	$- 3.28 * 10^{-6}$	$- 2.04 * 10^{-5}$	$1.38 * 10^{-5}$	$- 2.29 * 10^{-4}$	$- 2.36 * 10^{-3}$	$1.90 * 10^{-3}$			

Absence of a correlation between butterflies and food energy production

Contrary to the findings for total bird abundance and species richness, no significant interaction between butterflies and total food energy production at landscape level was detected (Fig. S6.1).

(A) Raw data



(B) Model predictions

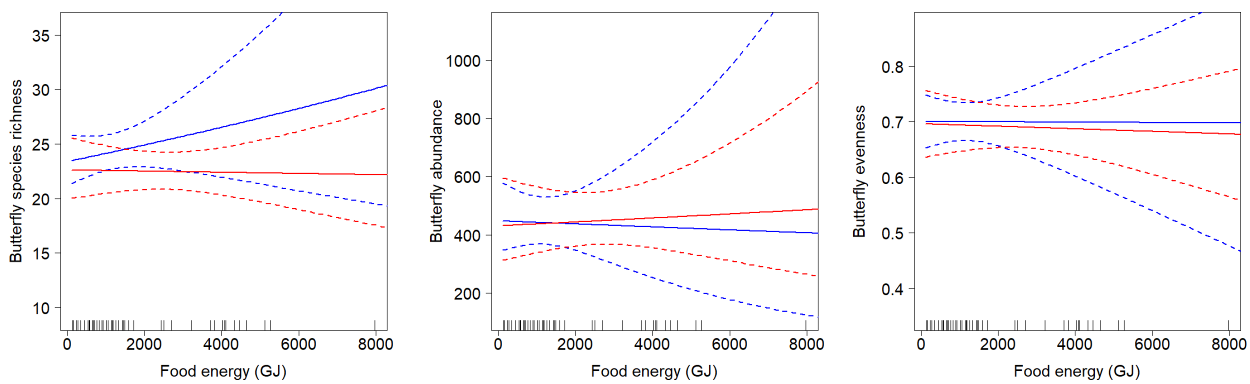
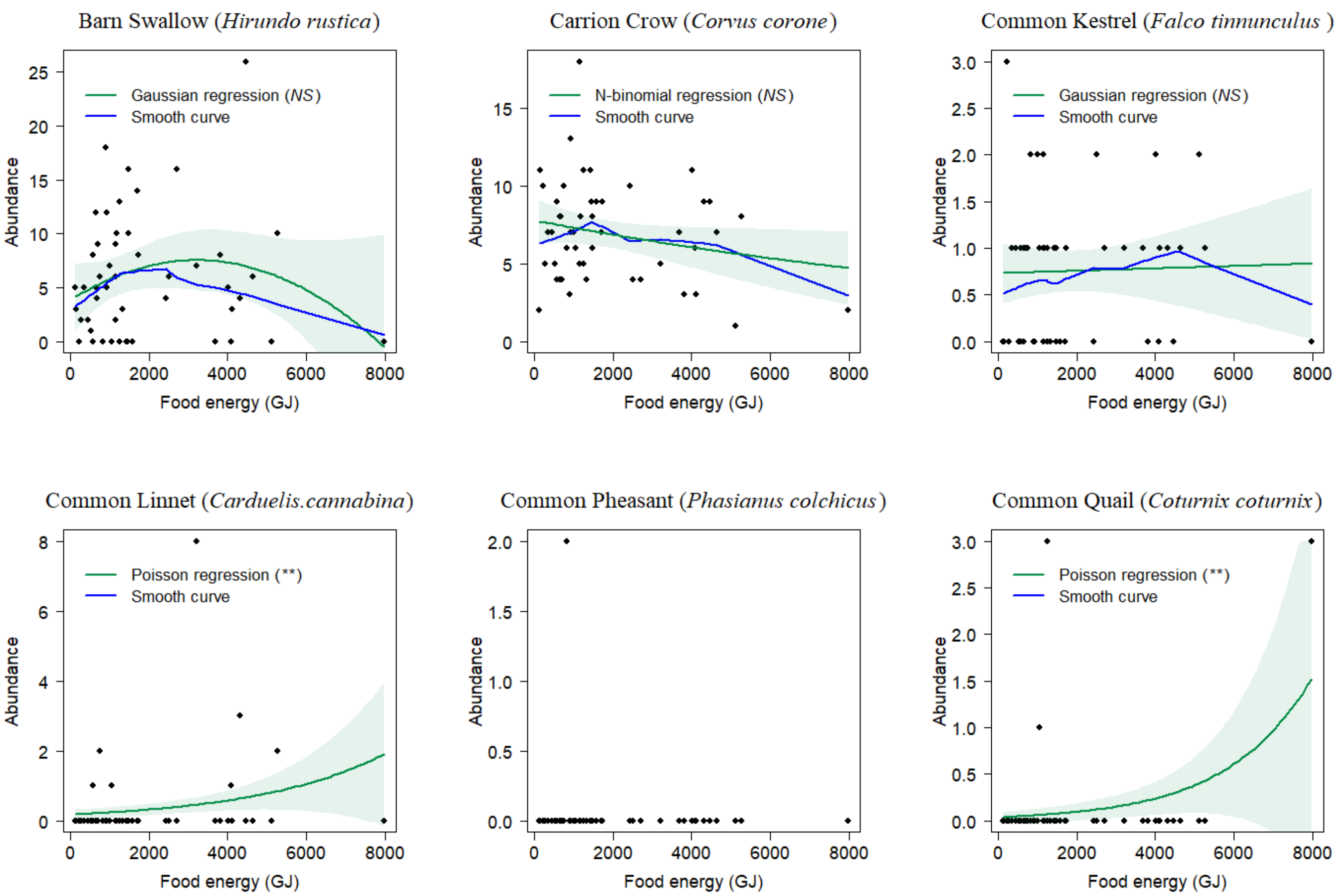
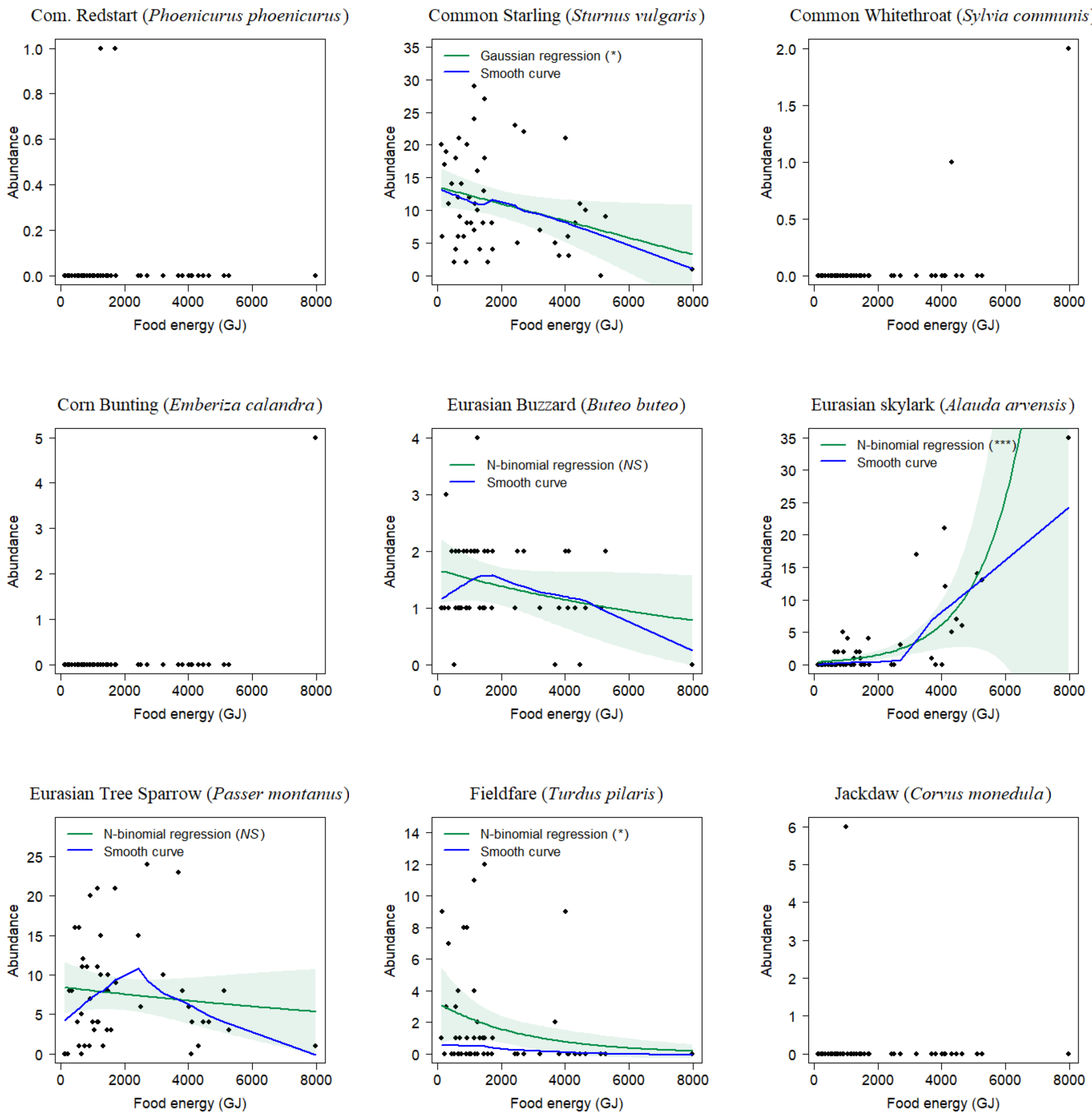


Figure. S6.1. Relationships between butterfly species richness, abundance and evenness and total food energy produced at landscape level (GJ from scenario 2). Figure (a) shows the raw data with the means of the imputed food energy values (defined as metabolizable energy for human consumption) as dots. Figure (b) shows the predicted regression lines for landscapes with different proportions of farmland 60 ha (blue) and 80 ha (red); respectively (all non-significant). Shown are pooled predictions with 95% confidence intervals from the n (= 50) models (interaction food energy* farmland area included as explanatory variable). The means of the imputed food energy values are shown as tick marks at the bottom.

S7 – Single species analyses

In the following two figures we present the responses of the 24 farmland bird species (Fig. S7.1) and 41 farmland butterfly species (Fig. S7.2) to increasing food energy production at landscape level (from scenario 2). For the species with three or more data points (= observations) the predicted regression (with 95% confidence interval) as well as the smooth curve are displayed. The type of predicted regression was selected based on AIC scores (with or without quadratic term) and the normality and homoscedasticity distributions of the residuals (linear model with Gaussian distribution, generalized linear model with Poisson distribution or negative binomial generalized linear model if overdispersion was present in the Poisson model). Asterisks indicate significant relationship at $P < 0.05$ (*), $P < 0.01$ (**) or $P < 0.001$ (***), and *NS* stands for not significant. The smooth curve was computed with the *lowess()* function in R which uses locally-weighted polynomial regression to calculate the interpolating points. The smoother span was set to 0.75 and the number of iterations to 4.




Com. Redstart (*Phoenicurus phoenicurus*)
Common Starling (*Sturnus vulgaris*)
Gaussian regression (*)
Smooth curve
Common Whitethroat (*Sylvia communis*)
Corn Bunting (*Emberiza calandra*)
Eurasian Buzzard (*Buteo buteo*)
N-binomial regression (*NS*)
Smooth curve
Eurasian skylark (*Alauda arvensis*)
N-binomial regression (***)
Smooth curve
Eurasian Tree Sparrow (*Passer montanus*)
N-binomial regression (*NS*)
Smooth curve
Fieldfare (*Turdus pilaris*)
N-binomial regression (*)
Smooth curve
Jackdaw (*Corvus monedula*)
Abundance
Food energy (GJ)

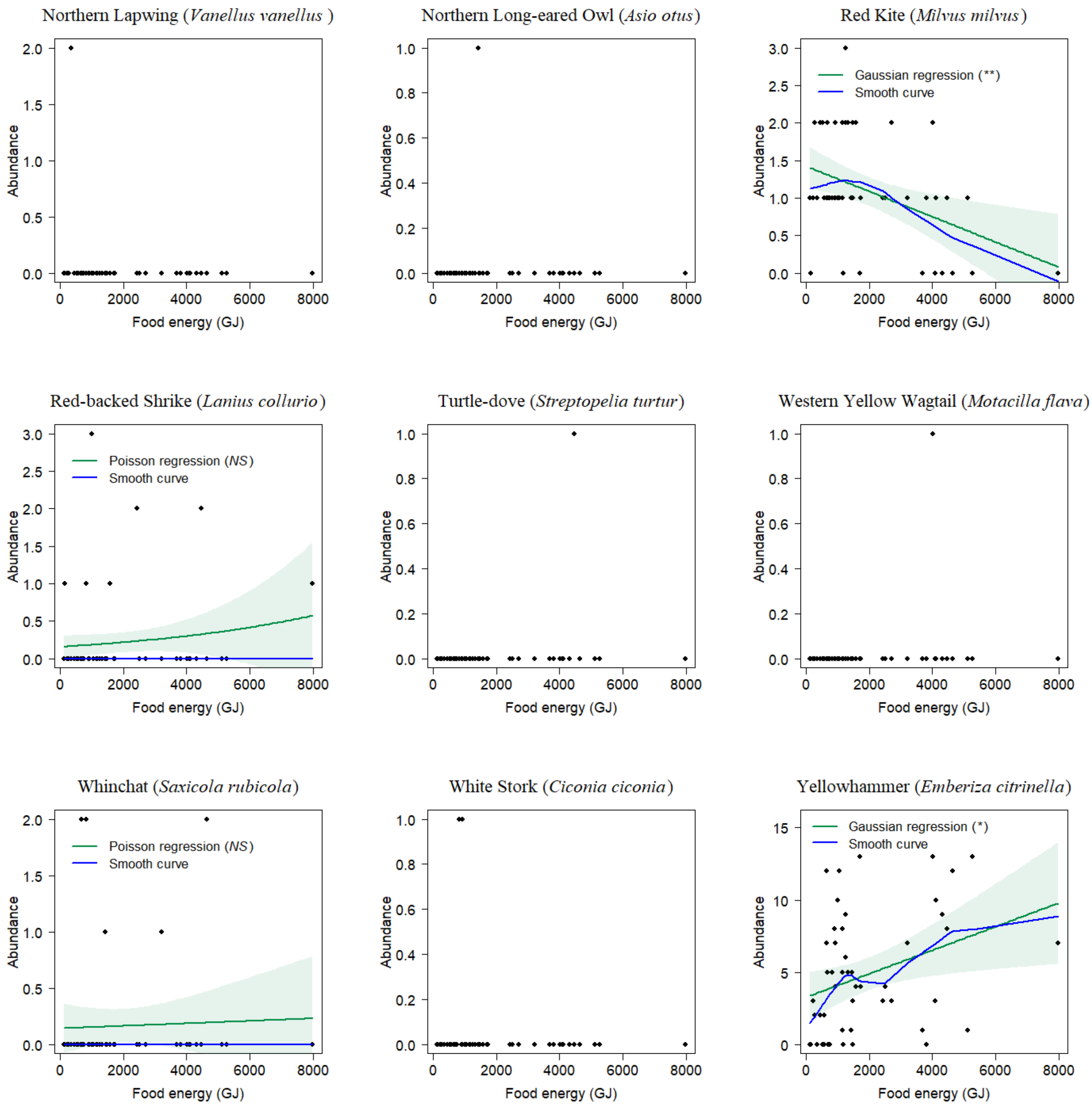
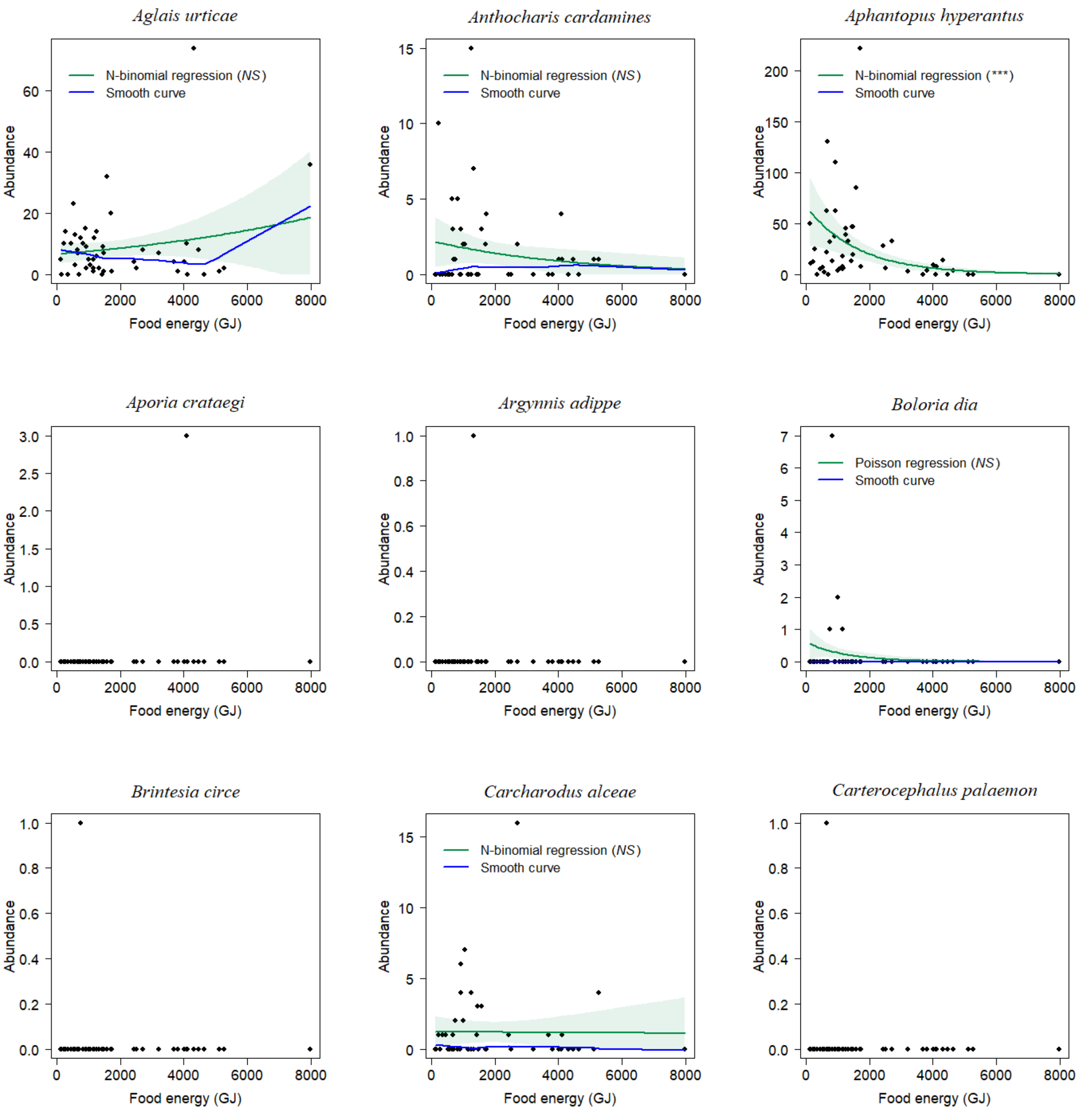
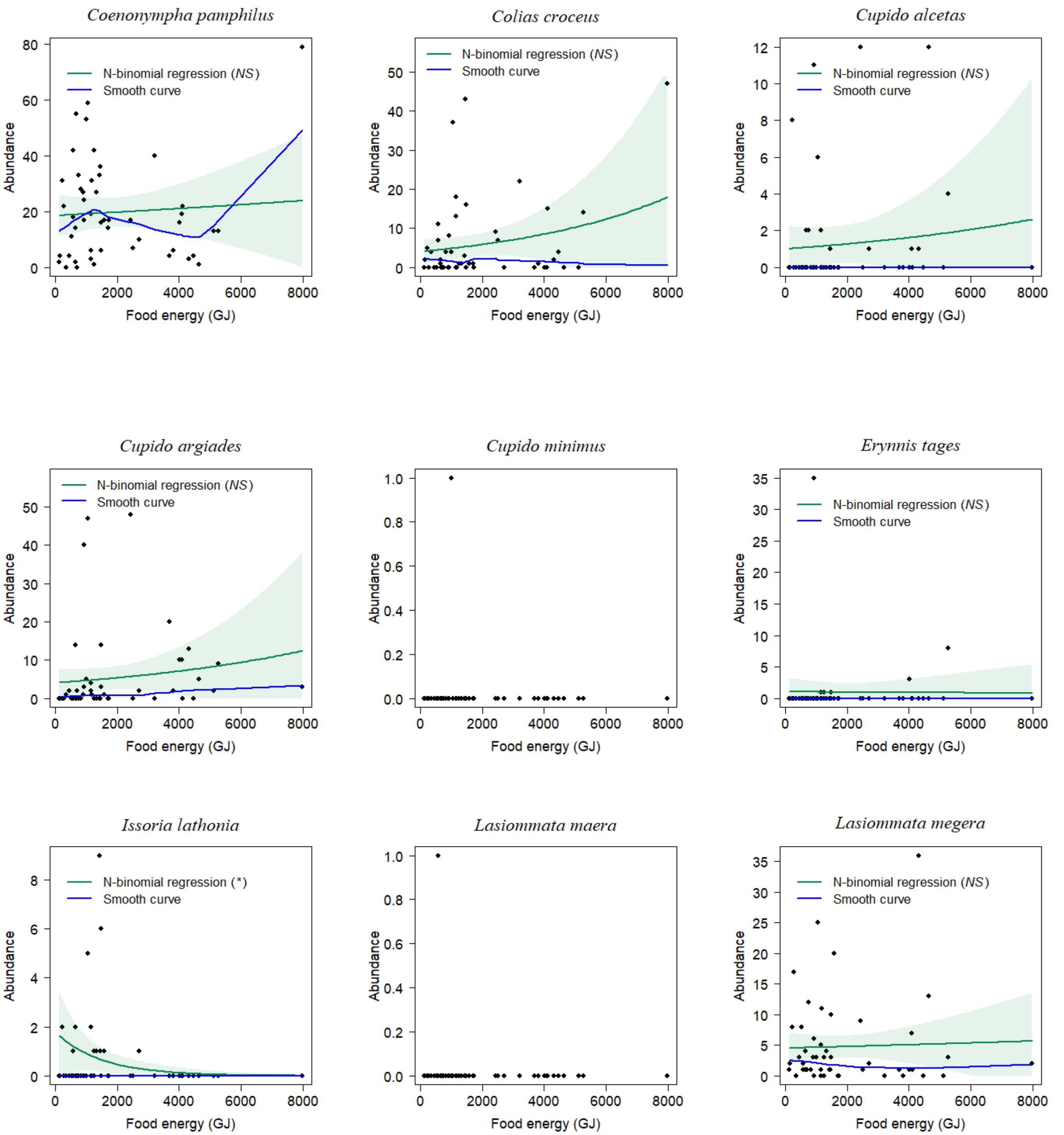
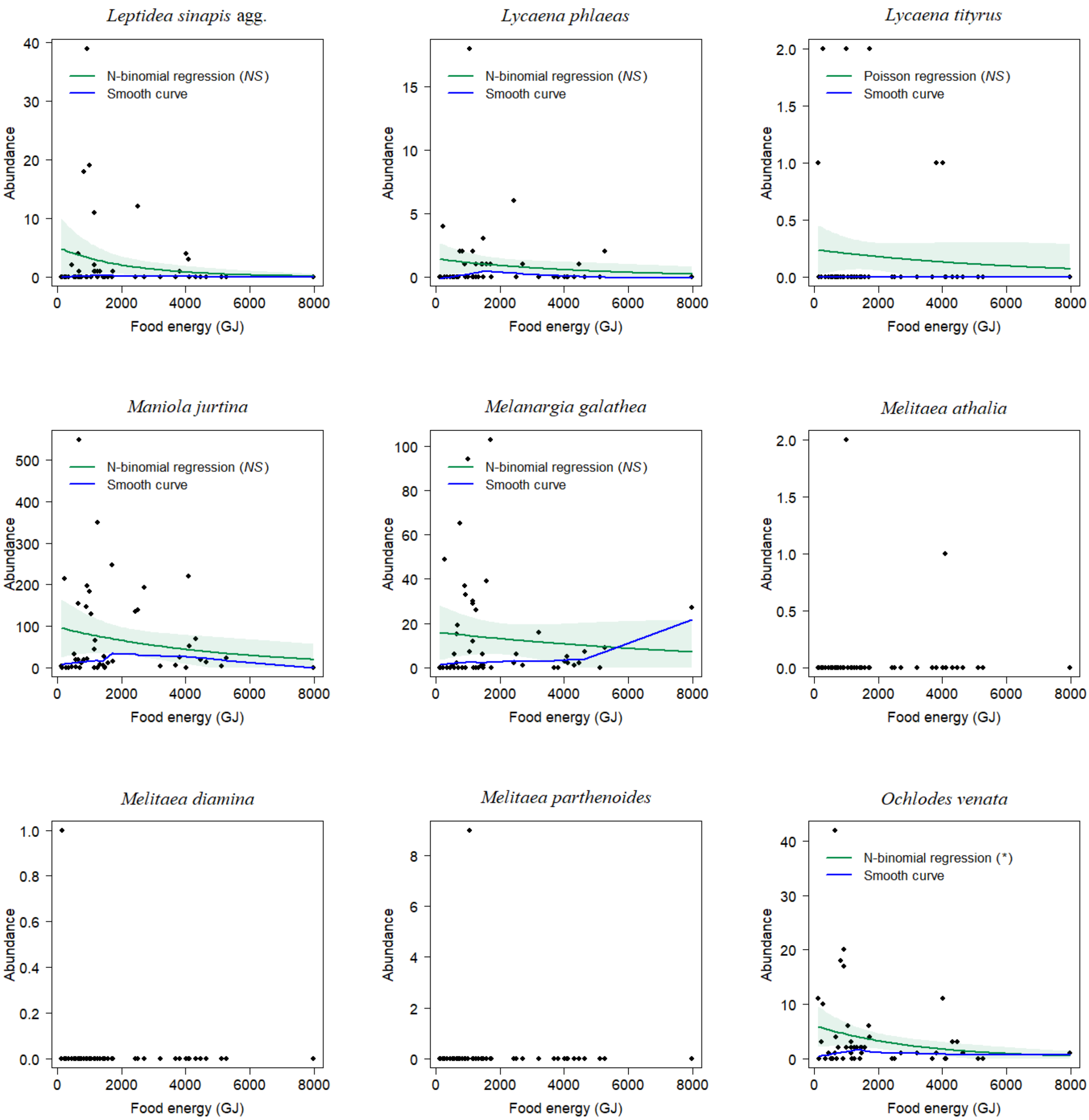
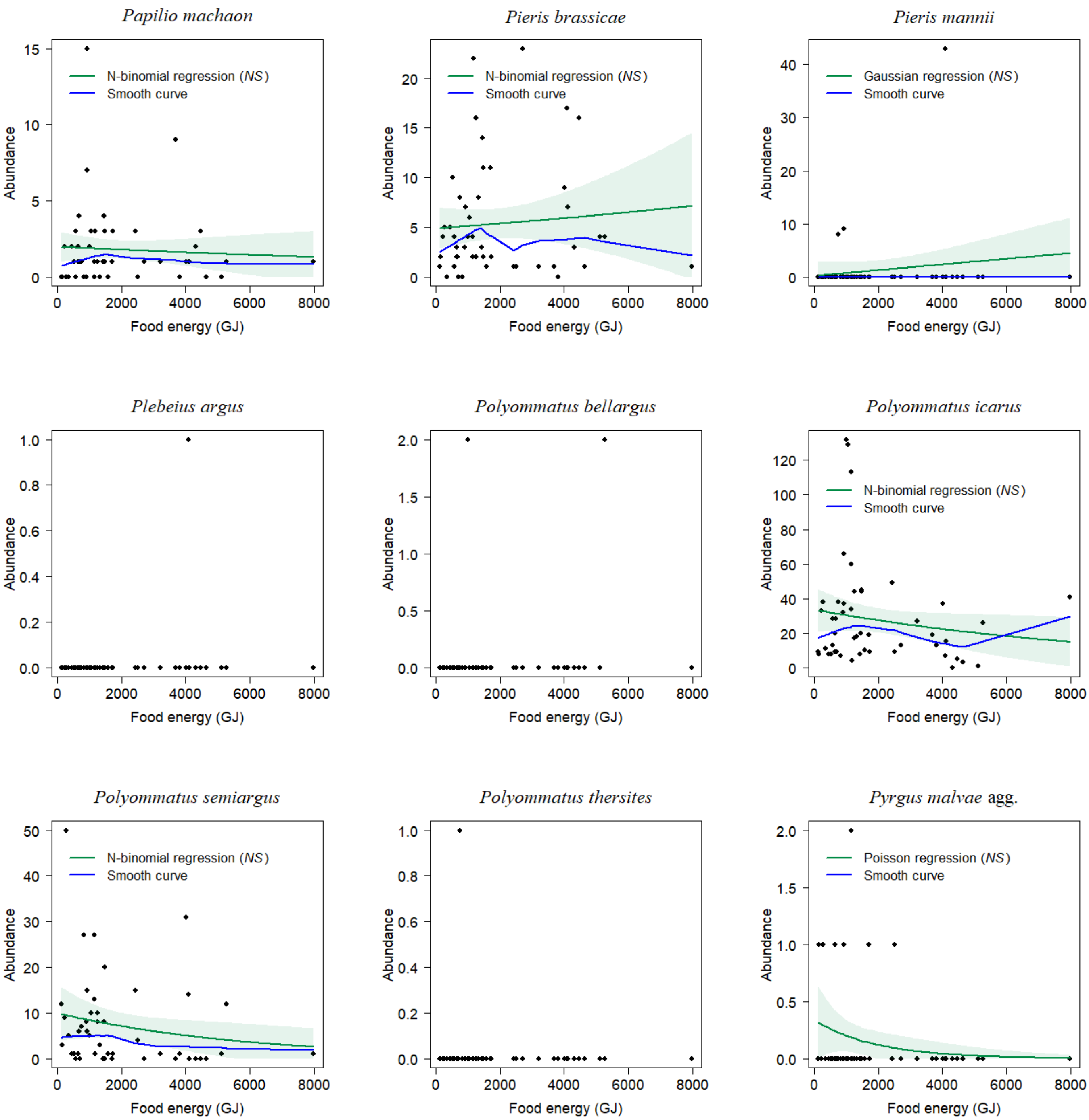


Figure. S7.1. Species-specific relationships between the abundance of the respective farmland bird species and total food energy produced at landscape level.


Aglais urticae
N-binomial regression (NS)
Smooth curve
Anthocharis cardamines
N-binomial regression (NS)
Smooth curve
Aphantopus hyperantus
N-binomial regression (***)
Smooth curve
Aporia crataegi
Argynnis adippe
Boloria dia
Poisson regression (NS)
Smooth curve
Brintesia circe
Carcharodus alceae
N-binomial regression (NS)
Smooth curve
Carterocephalus palaemon
Abundance
Food energy (GJ)


Coenonympha pamphilus
Colias croceus
Cupido alcetas
Cupido argiades
Cupido minimus
Erynnis tages
Issoria lathonia
Lasiommata maera
Lasiommata megera
N-binomial regression (NS)
N-binomial regression (*)
Smooth curve
Abundance
Food energy (GJ)


Leptidea sinapis agg.
N-binomial regression (NS)
Smooth curve
Abundance
Food energy (GJ)
Lycaena phlaeas
N-binomial regression (NS)
Smooth curve
Abundance
Food energy (GJ)
Lycaena tityrus
Poisson regression (NS)
Smooth curve
Abundance
Food energy (GJ)
Maniola jurtina
N-binomial regression (NS)
Smooth curve
Abundance
Food energy (GJ)
Melanargia galathea
N-binomial regression (NS)
Smooth curve
Abundance
Food energy (GJ)
Melitaea athalia
Abundance
Food energy (GJ)
Melitaea diamina
Abundance
Food energy (GJ)
Melitaea parthenoides
Abundance
Food energy (GJ)
Ochlodes venata
N-binomial regression (*)
Smooth curve
Abundance
Food energy (GJ)



Papilio machaon
N-binomial regression (NS)
Smooth curve
Pieris brassicae
N-binomial regression (NS)
Smooth curve
Pieris mannii
Gaussian regression (NS)
Smooth curve
Plebeius argus
Polyommatus bellargus
Polyommatus icarus
N-binomial regression (NS)
Smooth curve
Polyommatus semiargus
N-binomial regression (NS)
Smooth curve
Polyommatus thersites
Pyrgus malvae agg.
Poisson regression (NS)
Smooth curve
Abundance
Food energy (GJ)

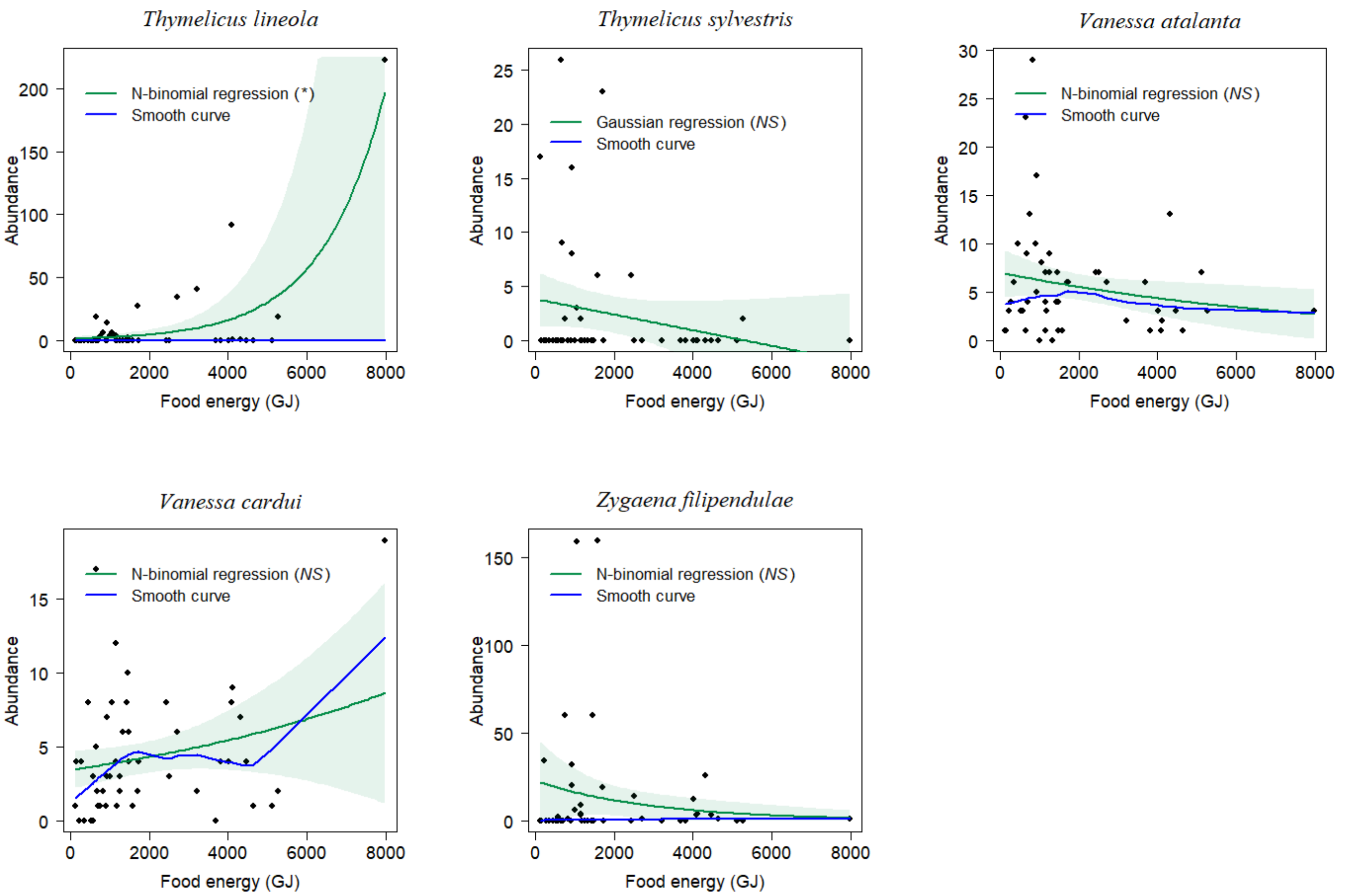


Figure S7.2. Species-specific relationships between the abundance of the respective farmland butterfly species and total food energy produced at landscape level.