Habitat fragmentation and connectivity loss affects the predation ecosystem service provided by birds and arthropods in calcareous grasslands.

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Abstract

Calcareous grasslands are one of the most species-rich habitats in Europe but are often fragmented and highly degraded because of agricultural intensification and the abandonment of traditional livestock farming. This leads to loss of biodiversity together with the degradation of ecosystem services, such as predation. In this study, we determined how local characteristics of grasslands (size and management), and landscape composition (connectivity and agri-environmental schemes) modulate predation by insectivorous birds and arthropods in calcareous grasslands. We conducted an experimental study in 96 calcareous grasslands in three countries (three different bioclimatic regions): 32 each in Spain, Germany and Estonia, using artificial caterpillars (10 pairs per grassland). Each pair consisted of one green and one brown caterpillar. Our results showed higher predation in Spain than in Germany and Estonia, as well as a positive effect of exposure height: the higher the caterpillars were placed, the higher the predation. In line with our expectations, we observed that bird predation was determined by predator abundance and landscape characteristics. The arthropod predation was negatively related to grassland size and positively related to management status of the grasslands. For both type of predations, the results show that fragmentation and loss of connectivity in European calcareous grasslands had negative effects on predation. In contrast, the results did not suggest that surrounding agri-environmental schemes were effective in compensating for the loss of predation services resulting from the reduced connectivity. In conclusion, our work demonstrates that improving connectivity favors predation by insectivorous birds and arthropods, suggesting that the conservation and restoration of calcareous grasslands, in addition to greatly favoring biodiversity, can lead to an increase in key ecosystem services such as predation and pest control.

Keywords: Agricultural intensification, agri-environmental schemes, dummy caterpillars, sentinel prey, farmland birds, habitat restoration, traditional livestock farming, connectivity, landscape.

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1. Introduction

Since the middle of the last century, European agricultural landscapes have changed dramatically due to the fast agricultural intensification (Matson et al., 1997; Winkler et al., 2021). Consequently, many of the natural and semi-natural habitats that characterized agricultural landscapes in the past have disappeared, or their area has been severely reduced (Matson et al., 1997; Pienkowski and Pain, 1997; Traba and Morales, 2019; Winkler et al., 2021). One important example is the loss of semi-natural grasslands either due to intensification through increased fertilizer use, grazing and mowing or through abandonment and the decline of traditional management (Shipley et al. 2024). This is also the case for calcareous grasslands, increasingly scarce habitats in European agricultural landscapes (WallisDeVries et al., 2002; Helm et al., 2006).

Calcareous grasslands are one of the most species-rich habitats in Europe, offering many niches for threatened species from different organism groups such as plants, insects and birds (Gazol et al., 2012; Kormann et al., 2015; Ernst et al., 2017). They are the result of extensive grazing and mowing regimes on dry calcareous soils (Poschlod and WallisDeVries, 2002) and are characterized by plant and animal communities that are particularly adapted to dry, nutrient-poor conditions (Öckinger et al., 2006; Kasari et al., 2016). However, nowadays most of the calcareous grasslands are fragmented and highly degraded because of agricultural intensification and the abandonment of traditional livestock farming (WallisDeVries et al., 2002; Helm et al., 2006; Gorris et al., 2024). Particularly, the loss of traditional agro-pastoral practices leads to shrub and forest encroachment, resulting in biotic homogenization (Gossner et al., 2016; Prangel et al., 2023; Gorris et al., 2024). This degradation and fragmentation of calcareous grasslands could have a strong negative impact on their biodiversity and thus, on the ecosystem services they have historically provided, such as predation (Steffan-Dewenter and Tscharntke, 2002; Bengtsson et al., 2019; Klaus et al., 2021; Prangel et al., 2023; Prangel et al., 2024). This could also have implications for agriculture, as crop fields in the landscape surrounding calcareous grasslands could benefit from higher pollinator abundances, predation rates and biological pest control due to spill-over of organisms from these highly diverse habitats (Blitzer et al. 2012; Maas et al., 2021; Vilumets et al., 2023).

At local scale, reduction in grassland size could have significant negative impacts on biodiversity and in particular for specialist and endangered species, both in terms of species richness and abundance (Olsen et al., 2018; Loos et al., 2021, Kirsch et al. 2024), and therefore on ecosystem services they provide (Klaus et al., 2021). Moreover,

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to minimize or reverse the effect of abandonment, different management measures are applied within some of these grasslands, such as grazing, shrub removal, ploughing, mowing, or a combination of them, while in others no management is applied at all (Kormann et al., 2015; Helbing et al., 2021; Prangel et al., 2024). This leads to a great diversity in the management and therefore conservation status of European calcareous grasslands (Kormann et al., 2015; Helbing et al., 2021; Prangel et al., 2024), which possibly also has implications for biodiversity and ecosystem services (Helbing et al., 2021; Prangel et al., 2023).

At landscape scale, the impact of fragmentation and the loss of habitat connectivity could be particularly negative for specialist and endangered species (Kormann et al., 2015; Olsen et al., 2018; Maas et al., 2021; Gallé et al., 2022; Kirsch et al. 2024), which could also lead to a decrease in predation service, due to the loss of potential predators. This effect may vary depending on the grassland size, with a stronger negative effect being more likely in smaller grasslands where landscape context may have a greater influence (Rösch et al., 2013). In this sense, the Common Agricultural Policy of the European Commission (hereafter CAP) supports the implementation of agri-environmental schemes (hereafter AES), such as organic farming, fallows, flower fields or extensive grassland management, aiming to conserve farmland biodiversity (Pe'Er et al., 2017), and contribute to mitigate the loss of ecosystem services. These AES could be grouped into two groups, non-productive measures such as fallow land, green strips or conservation grassland and productive measures such as organic farming, organic grassland or permanent grassland. Non-productive AES are not so well accepted by the farmers but considered to have more beneficial effects on biodiversity (Pe'Er et al., 2017). However, effects of AES are often only tested for single schemes, such as organic farming or fallow land (Schmidt et al., 2008; Winqvist et al., 2012), or AES are included in more general variables describing landscape composition, e.g based on landscape diversity (Gámez-Virués et al., 2015). To disentangle potentially diverging outcomes, effects of productive and non-productive AES on biodiversity and ecosystem functions and services should be analyzed separately.

A widely used method for the experimental study of predation is the use of dummy caterpillars made of modelling clay (Howe et al., 2009; Lövei and Ferrante, 2017; Roslin et al., 2017; Hernández-Agüero et al., 2020). This methodology allows to differentiate the imprints left on the dummy caterpillars by different taxa (e.g. birds, mammals, arthropods and gastropods) and to quantify and compare their predation rates (Roslin et al., 2017; Valdés-Correcher et al., 2022). Thus, the use of dummy caterpillars provides

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reliable and comparable data in a simple and single experiment (Roslin et al., 2017; Ferrante et al., 2024).

In this study, we aim to determine how local characteristics of grassland (size and management), and landscape composition (connectivity and area of productive and non-productive AES around target grasslands) modulate predation by birds and arthropods in calcareous grasslands. We used dummy caterpillars to estimate the effects of these local and landscape characteristics on predation by birds and arthropods. Our main hypotheses are: 1) bird and arthropod predation are positively associated with grassland connectivity and size; 2) productive AES will have negative or negligible effects on predation while non-productive AES, as they tend to promote natural vegetation habitats, will have positive effects on predation; 3) the effects will be different between regions depending on management measures implemented.

2. Material and methods

2.1. Study regions

We conducted the study in three European countries of different biogeographical regions; in Spain (Mediterranean region), Germany (continental region), and Estonia (boreal region). Therefore, the study sites cover the entire continental variability of calcareous grassland ecosystems in Europe (Fig. 1; more detailed descriptions of the study regions in Gorris et al., 2024). The study was carried out during May 2023.

2.2. Grassland selection and calculation of local and landscape management

In each country, we selected 32 calcareous grasslands. This selection was made from a pre-selection of over 100 calcareous grasslands of up to 10 hectares. We aimed at selecting 16 managed and 16 unmanaged grasslands. However, this was not possible in all countries, e.g. in Germany less than 16 unmanaged grasslands were available in the study region. The selection aimed to maximize variability in the following landscape-scale variables: connectivity, productive agri-environmental schemes (hereafter productive AES) and non-productive agri-environmental schemes (hereafter non-productive AES).

Connectivity was estimated as the percentage of area covered by other calcareous grasslands around the focal one, and the AES were estimated as the percentage covered by productive and non-productive agri-environmental schemes. All three

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variables were estimated within a 1km and 2km buffer around the border of each grassland. We categorized the AES based on whether they were applied to a field with productive purposes (e.g. organic farming) or to a field that was left unexploited (e.g. fallow), we provide detailed information about each category in Table A1, Appendix A. We calculated these environmental variables (connectivity and AES) using QGIS (QGIS.org, 2024) and R (R Core Team 2023) based on land use data available in each country for the year 2023: Unique Agrarian Statement/DUN and Regional Geographic Information System of Farming Land of the Generalitat de Catalunya in Spain; EELIS - Estonian Nature Information System of the Estonian Environment Agency and WFS map of Estonian organic areas in Estonia; and LEA portal of Lower Saxony (https://sla.niedersachsen.de/landentwicklung/LEA/) as well as IACS data (Integrated Administration and Control System) in Germany.

For each of the 32 selected grasslands, we also estimated a country-specific local management index. The aim of the local management index was to combine the intensity of different restoration and conservation measures (which are only available for managed sites) with the woody cover as an indicator for site abandonment (which is most relevant for not managed sites) into one variable for each of the study sites.

Restoration and conservation measures were collected differently in each country due to local context discrepancies and differences in source availability. They included a grazing index (Germany, Estonia) or a grazing category (Spain), continuity in grassland management (Estonia, Germany), time since restoration (Estonia) and regular shrub mowing (Germany). The abandonment variable woody cover was available in all three countries. In the case of Germany and Estonia, all variables except the woody cover were obtained by interviews with farmers. Detailed information on collection and calculation of restoration and conservation measures can be found in Appendix B.

To obtain one management index per site, we aimed at ranking the sites according to i) their restoration and management measures and ii) their abandonment state indicated by woody cover. In a first step, we used multivariate statistics in Germany and Estonia to reduce the dimensionality of the different restoration and conservation measures. Therefore, we built a specific Principal Component Analysis (PCA) model (Legendre & Legendre, 2012) for each of the two countries based on the available information about restoration activities (see Supplementary Material Table S2). PCAs were calculated using the vegan package (Oksanen et al., 2024) and variables were scaled for the calculation. PCA first axis (PC1) represented a proportion of 65.59% of the explained variance in Estonia and 41.76% in Germany and were in both cases positively correlated

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with all restoration and conservation measures (see supplementary material Fig. A1 and Fig. A2, Appendix A for more details). Thus, we extracted PC1 and ranked all sites per country based on their PC1 values, ranking the highest PC1 as the highest management value. For non-managed sites we assigned the lowest value, calculated as the average rank of all non-managed tied values. In Spain a PCA was not necessary, because only one management variable was available. Therefore, we ranked all sites in Spain based on their grazing category.

In a second step, we ranked the sites according to their woody cover in each country representing the state of abandonment (sites with the lowest shrub cover received the highest rank and sites with the highest shrub cover the lowest rank). Finally, we combined the ranks of restoration and conservation measures with the ranks of woody cover, by taking the mean of both for each site, resulting in the final management index.

2.3. Assessing predation with dummy caterpillars

The study on predation was carried out using dummy caterpillars. These caterpillars (25mm x 3mm) were made of two colors of Staedtler Modelling clay (Supplementary material, Figure S4): brown (Ref. Noris® 8421-7) and green (Ref. Noris® 8421-5; Meyer et al., 2019; Valdés-Correcher et al., 2019). A pair of caterpillars (one of each color) was closely attached to a shrub in a visible place using cyanoacrylate. We placed 10 pairs of dummy caterpillars on each grassland, on 10 different shrubs, at a height of 20 - 200 cm (mean = 82.8 cm; standard deviation = 27.7 cm). The caterpillars were installed in a moving posture (Supplementary material, Fig. A3, Appendix A). We decided not to place caterpillars on the ground because arthropod predation at ground level is predominant (Kuli-Révész et al., 2021) and we were focusing on predation by both birds and arthropods. In total, we installed 960 pairs of dummy caterpillars, 320 per country; of these caterpillars, 16 disappeared (2 in Spain, 8 in Germany and 6 in Estonia) and we did not consider them for the analysis. We recorded the height at which we placed each pair of caterpillars and average height of grassland was used as the height of exposure.

Caterpillars remained on the field for 7 days (Lövei, et al., 2017). After this time, we checked the caterpillars and noted all predation events detected. We classified predation events into four categories according to the predator marks/imprints: birds, arthropods, gastropods, and rodents (Valdés-Correcher, et al., 2022; Fig. A4, Appendix A). In all cases, whenever a predation event was detected, we took a photo of the caterpillar to unify criteria, as the sampling was carried out by different people in each country. All photos were reviewed by a single researcher (XC).

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2.4. Bird point counts

To determine whether predation by birds was related to bird abundance, we carried out two bird surveys in each grassland to estimate an index of bird abundance before and after the experiment. We conducted these surveys based on 10-minute census on the most central point of each grassland. We used the maximum number of individuals detected per species in one of the two surveys as an index of abundance for each species. Then, we classified each bird species by functional traits using the Avonet database (Tobias et al., 2022). We selected only invertivore or omnivore species typical for grasslands and shrublands, with a body mass under 150g and which did not feed in flight.

2.5. Statistical analysis

2.5.1. Color preferences

First, we analyzed differences in the predation recorded on the caterpillars with the different colors to provide methodological guidance for future studies (i.e. to avoid or control for color preferences). We fitted three generalized linear mixed models (GLMM) with a binomial error and a logit link function, for the binomial response variables (presence/absence) using the R package *lme4* (Bates et al., 2015); one for total predation, one for predation by birds and one for predation by arthropods. The fixed factors "caterpillar color" (brown/green) and "country" (Estonia/Germany/Spain) were included as explanatory variables and the grassland ID as random factor in all models.

2.5.2. Local and landscape-scale effects on predation

We compiled five local and three landscape-scale variables that were included as explanatory variables in our analyses (Table 1). As response variable, we used a double column response variable (predated pairs of caterpillars, not predated pairs of caterpillars). Combining the predation data for each pair of caterpillars (both colors) resulted in a better-balanced data set. Consequently, we counted a predation event when at least one of the caterpillars of the pair was predated (regardless of color).

We built four double column variables based on predator type: i) total predation, ii) predation by birds, iii) predation by arthropods, and iv) predation by gastropods. Predation by rodents was not considered, as it was an extremely scarce event (4 predated pairs of caterpillars out of 960). First, we evaluated differences in the predator type-specific predation between countries by fitting 4 binomial generalized linear models

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(GLMs, R package *lme4*; Bates et al., 2015), one per response variable, including height of exposure and country as explanatory variables.

Second, in the cases of bird and arthropod predation (the most common ones), we explored their relationship with local and landscape variables (Table 1). We fitted a GLM with a binomial error and a logit link function for each of these two predation variables. Prior to building the models, we checked for the intercorrelation of explanatory variables and found no highly correlated variables (absolute values of Pearson's correlation coefficient < 0.7).

For the bird predation model, the following explanatory variables were used: country, grassland size, height of exposure, management index, abundance of invertivore birds, abundance of omnivore birds, connectivity in 2 km, percentage of productive AES in 2 km, and percentage of non-productive AES in 2 km (Table A3, Appendix A). We used landscape variables in a 2 km buffer around the grasslands because of the high mobility of birds (McKenzie et al., 2013). We also included the two-way interactions of each variable with country, except for connectivity, which had very different ranges across countries and made interactions problematic. Moreover, we added the interaction between non-productive AES and connectivity to determine if the impact of connectivity loss was mitigated by the implementation of non-productive AES. Finally, we included the interaction between connectivity and grassland size to assess whether the effect of connectivity loss was influenced by the grassland size. Starting from this model, we made a model selection using the *dredge* function of the *MuMIn* package in R (Barton, 2009), which compares the Akaike information criterion (AIC) values of all models. We selected the best model and provided information on all models with ΔAICc ≤ 2 in Appendix C.

Regarding the model of arthropod predation, we used landscape variables estimated in a 1 km buffer around the grasslands, since the distance that the most common predatory arthropods (ants, beetles and wasps) tend to cover is usually shorter (Gámez-Virués et al., 2015). For the model we included as explanatory variables: country, grassland size, height of exposure, management index, connectivity in 1 km, percentage of productive AES in 1 km, and percentage of non-productive AES in 1 km. We also added the two-way interactions of each variable with country, except for connectivity, the interactions between non-productive AES and connectivity, and the interaction between connectivity and grassland size (Table A3, Appendix A). We used the same model selection process than above using *dredge* function of *MuMIn* package in R (Barton, 2009). Similarly, we

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selected the best model and provided information on all models with ΔAICc ≤ 2 in Appendix C.

All analyses were carried out with R v4.3.2 (R Core Team 2023), and graphics were produced with the package *ggplot2* of R (Wickham 2016). We computed Tukey HSD post hoc test for comparisons between countries within models using the *lsmeans* R package (Russell 2016), and we used the function Anova of *car* R package (Fox et al., 2012) to extract statistical results from models.

3. Results

Our results on the effect of caterpillar color showed that there were differences in predation between caterpillars of different colors, with brown caterpillars being more often predated (X^2_1 = 4.59, p < 0.05). However, when analyzed by predator type, these differences were not significant (Fig. A5, Appendix A).

3.1. Differences in the predation between countries

There were pronounced differences in predation between countries. We found that total predation, predation by birds and predation by arthropods were much higher in Spain than in Germany and Estonia (Figure 2; Table A4, Appendix A). However, we did not observe differences in predation between Estonia and Germany (Figure 2; Table A4, Appendix A). In the case of predation by gastropods, no significant differences were observed between countries (Table A4, Appendix A). In addition, the results showed that birds were the predominant predators in all countries, followed by arthropods (Figure 2). Besides, we also found that height of exposure seemed to have a positive effect on predation, although this was only marginally significant (X^2_1 = 3.34, p = 0.07; Fig. A6, Appendix A). This positive effect of installation height was significant for predation by birds (X^2_1 = 5.40, p < 0.05), but not for predation by arthropods (X^2_1 = 1.40, p = 0.24) and gastropods (X^2_1 = 0.03, p = 0.86; Fig. A6, Appendix A).

3.2. Local and landscape effects on bird predation

Regarding the predation by birds, the best model included as explanatory variables: country, height of exposure, abundance of invertivore birds, connectivity, and percentage of productive AES (Table A3, Appendix A). We found significant positive effects of invertivore bird abundance (X^2_1 = 11.38, p < 0.001) and connectivity (X^2_1 = 4.79, p < 0.05), a significant negative effect of productive AES (X^2_1 = 5.96, p < 0.05), and

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a marginally significant positive effect of the height of exposure (X^2_1 = 2.88, p = 0.09; Fig. 3). Grassland size did not appear to affect predation, nor did it modulate the effect of connectivity on predation, as both variables were rejected during model selection. Likewise, the management index and non-productive AES did not appear to affect bird predation. Finally, the interactions with country were not significant, indicating no substantial differences in the effect of the local and landscape-scale variables across different countries. Other models with a ΔAICc ≤ 2 included other variables (Appendix C) but in all cases the effect of those variables was not significant, and the effect of the above-mentioned variables was constant in all models.

3.3. Local and landscape effects on arthropod predation

The best model for arthropod predation included as explanatory variables the country, grassland size, height of exposure, management index, connectivity in 1 km, percentage of non-productive AES in 1 km, and the interaction between height of exposure and country and between connectivity and grassland size (Table A3, Appendix A).

Our results revealed that predation by arthropods was influenced by a broader range of factors than predation by birds, including some important interactions (Fig. 4 and Fig. 5). At local scale, predation by arthropods was affected by grassland size, the management index and the height of exposure, the later in interaction with country (Fig. 4). Grassland size showed a negative effect (X^2_1 = 4.62, p < 0.05; Fig. 4a) and management index a positive effect on arthropod predation (X^2_1 = 3.62, p = 0.06; Fig. 4b). Moreover, height of exposure showed a positive effect in Germany, and no effect in Spain and Estonia (Fig 4c). In case of arthropod predation, we also observed an interaction effect of connectivity and grassland size (Fig. 5b). Connectivity had a positive effect on predation in large grasslands (Fig. 5b, 90% percentile), but no effect in medium and small grasslands (Fig. 5b, median and 10% percentile). At the landscape level, we also found a negative effect of non-productive AES on arthropod predation (X^2_1 = 5.61, p < 0.05; Fig. 5a).

According to model selection, there were other two models with a ΔAICc ≤ 2, both very similar to the best model (Appendix C). The third model was the most complex (Appendix C), including to the best model the interaction between non-productive AES and country without a significant effect, but in this model the positive effect of the management index was significant (X^2_1 = 4.15, p < 0.05).

4. Discussion

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We found that predation on calcareous grasslands is affected by multiple local and landscape variables. Concerning grassland local management and restoration, we found that a better conservation status favors predation by arthropods but does not seem to affect predation by birds. The latter, as expected, was found to be closely linked to the abundance of insectivorous birds. Importantly, we could also demonstrate that landscape composition and especially grassland connectivity play an important role to enhance predation on calcareous grasslands. Surprisingly, we found that both AES (productive ones for birds and non-productive ones for arthropods) decreased the predation within the grasslands.

Consistent with previous studies, our data showed that dummy caterpillar color significantly influences the probability of predation (Zvereva et al., 2019; Hernández-Agüero et al., 2020; Roeder et al., 2023). In calcareous grasslands within an agricultural mosaic landscape, we found that brown dummy caterpillars were more heavily predated. This is in line with previous works in Europe, which indicates a slight preference for dark-colored caterpillars (Zvereva et al., 2019; Hernández-Agüero et al., 2020). However, this preference seems to be determined by predator species and may vary considerably with geographic region, since in the United States and in tropical regions, other patterns of preference for green or light colors have been described (Zvereva et al., 2019; Roeder et al., 2023). These data suggest that it may be beneficial, especially when working in different regions, to use groups of dummy caterpillars of different colors as a study unit (pairs in this study), which increases the probability of predation and thus facilitates data collection.

Moreover, we found that predation was significantly higher in Spain compared to Estonia and Germany, with no significant difference between the latter two countries. On the one hand, this could be due to a higher abundance of predators, both birds and arthropods, which seems to be the case for invertivore birds (e.g. warblers) and some arthropod groups (e.g. wasps and ants) in Spain (pers. obs.). On the other hand, these differences may also be due to differences in grassland plant composition and structure (Duckworth et al., 2020), which is likely to lead to substantial differences in the predator community between regions (Woodcock and Pywell, 2010). These differences are especially marked between the grasslands of Spain and those of Germany and Estonia. The former are drier and when shrubs are present, they are mostly small (<1 m, e.g. *Salvia rosmarinus*), whereas in Germany and Estonia grasslands are more humid, have herbaceous species and taller shrubs (>1.5 m, e.g. *Prunus spinosa*, *Juniperus communis* or *Rosa canina*). We also observed that exposure height significantly influences predation, which to our knowledge was not previously described. This information should

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be of great importance for the design of future studies and should be considered when comparing predation estimated in different studies with different heights of exposure.

Looking at local environmental factors that modulate predation, we could confirm a strong relationship between predation and predator abundance (Bereczki et al., 2014; Meyer et al., 2019), although this could only be tested in birds. In addition, grassland size (negative effect) and management (positive effect) influenced predation by arthropods. Thus, the results confirmed that, at least for arthropods, the management and therefore the conservation status of the grasslands is important for predation (Prangel et al., 2023). As for other ecosystem services such as pollination (Prangel et al., 2023; 2024), restored and well managed grasslands provide higher rates of predation ecosystem service. On the other hand, contrary to expectations, higher predation was detected in small grasslands. This unexpected result may be due to an edge effect (Kuli-Révész et al., 2021), with more predators on the edges and a higher edge/area ratio in small grasslands. The impact of edge effects on arthropod predation, along with its influence on interspecific interactions and the distribution of arthropod functional traits, is well-documented (Murphy et al., 2016; Wimp et al., 2019; Gallé et al., 2020). In the case of birds, neither grassland size nor management index were included in the final model and were not significant in other models, so they were not considered to be relevant for predation. This indicates that predation by birds in calcareous grasslands is not so much determined by local changes, but more by the landscape context.

At the landscape level, both connectivity and proportion of AES showed significant effects on bird and arthropod predation, with opposite trends for the different organism groups. Connectivity increased the predation of both arthropods and birds, although in the case of arthropods this effect was only observed in larger grasslands. Surprisingly, this interaction between connectivity and grassland size in arthropods is the opposite of that described previously in the literature (Rösch et al., 2013), where a greater effect of connectivity on species richness in small-sized grasslands was found. Another study on pollinators found no interactive effects between habitat size and connectivity (Kirsch et al., 2024). These differences could also be related to the connectivity indices used, since Rösch et al. (2013) and Kirsch et al. (2024) used Hanski's connectivity, and we used the surface percentage around the grassland. This relationship may also be influenced by the edge effect (Kuli-Révész et al., 2021). By contrast, higher percentages of AES reduced the predation: Productive AES in the case of bird predation and non-productive AES in the case of arthropod predation. This could indicate that these AES do not provide as many predators as the calcareous grasslands and instead provide trophic resources and therefore the predation decreases by dilution. In any case, our data do not indicate

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interactions between AES and connectivity, AES do, therefore, not compensate for the decrease in predation caused by the loss of connectivity. However, as we grouped several AES into two categories, i.e. productive and non-productive AES, potential positive effects of single measures on predation cannot be ruled out. Probably non-productive and permanent AES (semi-natural permanent habitats) can have the most beneficial effect on predation. They could perform like the calcareous grasslands themselves, as long as they have adequate time to naturalize and be colonized (Maas et al., 2021; Kirsch et al. 2024).

In conclusion, this study demonstrated that fragmentation and loss of connectivity in European calcareous grasslands not only have negative effects on biodiversity but also on the ecosystem functions that these natural habitats provide within the agricultural landscape, such as predation, which is an important function for biological pest control in agricultural crops. Likewise, the results showed that predation is determined by predator abundance and for some predators, such as arthropods, by grassland size and conservation status of grasslands. In contrast, at least in this study, the results did not suggest that AES are effective in compensating for the loss of the predation function resulting from the fragmentation and connectivity loss of calcareous grasslands. Therefore, to improve predation in the agricultural landscapes, grassland connectivity should increase and the conservation and restoration of calcareous grasslands.

Authors' contributions

Xabier Cabodevilla: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing.

Gerard Bota: Conceptualization, Funding acquisition, Methodology, Investigation, Formal analysis, Resources, Writing – review & editing.

Juan Traba: Conceptualization, Funding acquisition, Methodology, Investigation, Formal analysis, Resources, Writing – review & editing.

Annika Hass: Conceptualization, Funding acquisition, Methodology, Investigation, Writing – review & editing.

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This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

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David Giralt: Conceptualization, Funding acquisition, Methodology, Investigation, Formal analysis, Resources, Writing – review & editing.

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Appendix A, Appendix B and Appendix C. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: XXXXX

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

References

Barton, K., 2009. MuMIn: multi-model inference. http://r-forge. r-project. org/projects/mumin/.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P.J., Smith, H.G., Lindborg, R., 2019. Grasslands-more important for ecosystem services than you might think. Ecosphere, https://doi.org/10. 10.1002/ecs2.2582

Bereczki, K., Ódor, P., Csóka, G., Mag, Z., Báldi, A., 2014. Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. Forest Ecology and Management, 327, 96-105. https://doi.org/10.1016/j.foreco.2014.05.001

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agriculture, Ecosystems & Environment, 146(1), 34-43.

Duckworth, J.C., Bunce, R.G.H., Malloch, A.J.C., 2000. Vegetation-environment relationships in Atlantic European calcareous grasslands. Journal of Vegetation Science, 11(1), 15-22. https://doi.org/10.2307/3236770

Ernst, L.M., Tscharntke, T., Batáry, P., 2017. Grassland management in agricultural vs. forested landscapes drives butterfly and bird diversity. Biological Conservation, 216, 51-59.

Ferrante, M., Howe, A.G., Lövei, G.L., 2024. Experimental considerations support the use of artificial sentinel prey—a comment on Rodriguez-Campbell et al. Journal of Biogeography. https://doi.org/10.1111/jbi.14978

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Heiberger, R., 2012. Package 'car'. Vienna: R Foundation for Statistical Computing, 16(332), 333.

Gallé, R., Geppert, C., Földesi, R., Tscharntke, T., Batáry, P., 2020. Arthropod functional traits shaped by landscape-scale field size, local agri-environment schemes and edge effects. Basic and Applied Ecology, 48, 102-111. https://doi.org/10.1016/j.baae.2020.09.006

Gallé, R., Korányi, D., Tölgyesi, C., Lakatos, T., Marcolin, F., Török, E., Révész, K., Szabó, A.R., Torma, A., Gallé-Szpisjak, N., Marja, R., Szitár, K., Deák, B., Batáry, P., 2022. Landscape-scale connectivity and fragment size determine species composition of grassland fragments. Basic and Applied Ecology, 65, 39-49. https://doi.org/10.1016/j.baae.2022.10.001

Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N.K., Klein, A.M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M.,

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

Tscharntke, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. Nature communications, 6(1), 8568. https://doi.org/10.1038/ncomms9568

Gazol, A., Tamme, R., Takkis, K., Kasari, L., Saar, L., Helm, A., Pärtel, M., 2012. Landscape-and small-scale determinants of grassland species diversity: direct and indirect influences. Ecography, 35(10), 944-951.

Gorris, P., Bodin, Ö., Giralt, D., Hass, A. L., Reitalu, T., Cabodevilla, X., Hannappel, I., Helm, A., Prangel, E., Westphal, C., 2024. Socio-ecological perspective on European semi-natural grassland conservation and restoration: key challenges and future pathways. Available at SSRN 4909041. https://doi.org/10.2139/ssrn.4909041

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L.R., Jung, K., Keyel, A.C., Klein, A.M., Klemmer, S., Krauss, J., Lange, M., Müller, J., Overmann, J., Pašalić, E., Penone, C., Perović, D.J., Purschke, O., Schall, P., Socher, S.A., Sonnemann, I., Tschapka, M., Tscharntke, T., Türke, M., Venter, P.C., Weiner, C.N., Werner, M., Wolters, V., Wurst, S., Westphal, C., Fischer, M., Weisser, W.W., Allan, E., 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature, 540(7632), 266-269. https://doi.org/10.1038/nature20575

Helbing, F., Fartmann, T., Poniatowski, D., 2021. Restoration measures foster biodiversity of important primary consumers within calcareous grasslands. Biological Conservation, 256, 109058. https://doi.org/10.1016/j.biocon.2021.109058

Helm, A., Hanski, I., Pärtel, M., 2006. Slow response of plant species richness to habitat loss and fragmentation. Ecology letters, 9(1), 72-77.

Hernández-Agüero, J. A., Polo, V., García, M., Simón, D., Ruiz-Tapiador, I., Cayuela, L., 2020. Effects of prey colour on bird predation: an experiment in Mediterranean woodlands. Animal Behaviour, 170, 89-97. https://doi.org/10.1016/j.anbehav.2020.10.017

Howe, A., Lövei, G.L., Nachman, G., 2009. Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomologia Experimentalis et Applicata, 131(3), 325-329.

Kasari, L., Saar, L., de Bello, F., Takkis, K., Helm, A., 2016. Hybrid ecosystems can contribute to local biodiversity conservation. Biodiversity and conservation, 25, 3023-3041.

Kirsch, F., Hass, A., Alfert, T., Westphal, C., 2024. Landscape diversity, habitat connectivity, age and size determine the conservation value of limestone quarries for diverse wild bee communities. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.14820

Klaus, F., Tscharntke, T., Uhler, J., Grass, I., 2021. Calcareous grassland fragments as sources of bee pollinators for the surrounding agricultural landscape. Global Ecology and Conservation, 26, e01474. https://doi.org/10.1016/j.gecco.2021.e01474

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

Kormann, U., Rösch, V., Batáry, P., Tscharntke, T., Orci, K. M., Samu, F., Scherber, C., 2015. Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. Diversity and Distributions, 21(10), 1204-1217.

Kuli-Révész, K., Korányi, D., Lakatos, T., Szabó, Á. R., Batáry, P., Gallé, R., 2021. Smaller and isolated grassland fragments are exposed to stronger seed and insect predation in habitat edges. Forests, 12(1), 54. https://doi.org/10.3390/f12010054

Legendre, P., Legendre L., 2012. Numerical ecology. Elsevier. ISBN: 9780444538680

Loos, J., Krauss, J., Lyons, A., Föst, S., Ohlendorf, C., Racky, S., Röder, M., Hudel, L., Herfert, V., Tscharntke, T., 2021. Local and landscape responses of biodiversity in calcareous grasslands. Biodiversity and Conservation, 30, 2415-2432. https://doi.org/10.1007/s10531-021-02201-y

Lövei, G. L., Ferrante, M., 2017. A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. Insect Science, 24(4), 528-542. https://doi.org/10.1111/1744-7917.12405

Maas, B., Brandl, M., Hussain, R. I., Frank, T., Zulka, K. P., Rabl, D., Walcher, R., Moser, D., 2021. Functional traits driving pollinator and predator responses to newly established grassland strips in agricultural landscapes. Journal of Applied Ecology, 58(8), 1728-1737. https://doi.org/10.1111/1365-2664.13892

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science, 277(5325), 504-509.

McKenzie, A.J., Emery, S.B., Franks, J.R., Whittingham, M.J., 2013. Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate?. Journal of Applied Ecology, 50(5), 1274-1280. https://doi.org/10.1111/1365-2664.12122

Meyer, S.T., Heuss, L., Feldhaar, H., Weisser, W.W., Gossner, M.M., 2019. Land-use components, abundance of predatory arthropods, and vegetation height affect predation rates in grasslands. Agriculture, Ecosystems & Environment, 270, 84-92. https://doi.org/10.1016/j.agee.2018.10.015

Murphy, S.M., Battocletti, A.H., Tinghitella, R.M., Wimp, G.M., Ries, L., 2016. Complex community and evolutionary responses to habitat fragmentation and habitat edges: what can we learn from insect science?. Current Opinion in Insect Science, 14, 61-65. https://doi.org/10.1016/j.cois.2016.01.007

Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biological conservation, 133(3), 291-300.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D.,

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2024. Package ‘vegan’. Community ecology package, version 2.6-8

Olsen, S.L., Evju, M., Endrestøl, A., 2018. Fragmentation in calcareous grasslands: species specialization matters. Biodiversity and Conservation, 27, 2329-2361. https://doi.org/10.1007/s10531-018-1540-z

Pe'Er, G., Zinngrebe, Y., Hauck, J., Schindler, S., Dittrich, A., Zingg, S., Tscharntke, T., Oppermann, R., Sutcliffe, L.M.E., Sirami, C., Schmidt, J., Hoyer, C., Schleyer, C., Lakner, S., 2017. Adding some green to the greening: Improving the EU's Ecological Focus Areas for biodiversity and farmers. Conservation letters, 10(5), 517-530. https://doi.org/10.1111/conl.12333

Pienkowski, M.W., Pain, D.J., 1997. Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation. San Diego: Academic Press.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. Biological Conservation, 104(3), 361-376.

Prangel, E., Kasari-Toussaint, L., Neuenkamp, L., Noreika, N., Karise, R., Marja, R., Ingerpuu, N., Kupper, T., Keerberg, L., Oja, E., Meriste, M., Tiitsaar, A., Ivask, M., Helm, A., 2023. Afforestation and abandonment of semi-natural grasslands lead to biodiversity loss and a decline in ecosystem services and functions. Journal of Applied Ecology, 60(5), 825–836. https://doi.org/10.1111/1365-2664.14375

Prangel, E., Reitalu, T., Neuenkamp, L., Kasari-Toussaint, L., Karise, R., Tiitsaar, A., Soon, V., Kupper, T., Meriste, M., Ingerpuu, N., Helm, A., 2024. Restoration of semi-natural grasslands boosts biodiversity and re-creates hotspots for ecosystem services. Agriculture, Ecosystems & Environment, 374, 109139. https://doi.org/10.1016/j.agee.2024.109139

QGIS.org, 2024. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team, 2023. A Language and Environment +or Statistical Computing. R Foundation +or Statistical Computing, Vienna, Austria. URL. https://www.Rproject. org/.

Roeder, K.A., Dorland, M.S., Daniels, J.D., 2023. Importance of color for artificial clay caterpillars as sentinel prey in maize, soybean, and prairie. Entomologia Experimentalis et Applicata, 171(1), 68-72. https://doi.org/10.1111/eea.13251

Rösch, V., Tscharntke, T., Scherber, C., Batary, P., 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. Journal of Applied Ecology, 50(2), 387-394. https://doi.org/10.1111/1365-2664.12056

Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A., Barrio, I.C., Basset, Y., Boesing, A.L., Bonebrake, T.C, Cameron, E.K., Dáttilo, W., Donoso, D.A., Drozd, P., Gray, C.L., Hik, D.S., Hill, S.J., Hopkins, T., Huang, S., Koane, B., Laird-Hopkins, B., Laukkanen, L., Lewis, O.T., Milne, S., Mwesige, I., Nakamura, A., Nell, C.S.,

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

Nichols. E., Prokurat, A., Sam, K., Schmidt, N.M., Slade, A., Slade, V., Suchanková, A., Teder, T., Van Nouhuys, S., Vandvik, V., Weissflog, A., Zhukovich, V., Slade, E.M., 2017. Higher predation risk for insect prey at low latitudes and elevations. Science, 356(6339), 742-744.

Russell, V.L., 2016. Least-squares means: the R package lsmeans. J Stat Softw 69:1–33. https://doi.org/10.18637/jss.v069.i01

Schmidt, M.H., Rocker, S., Hanafi, J., Gigon, A., 2008. Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. Biodiversity and conservation, 17, 3003-3012. https://doi.org/10.1007/s10531-008-9412-6

Shipley, J.R., Frei, E.R., Bergamini, A., Boch, S., Schulz, T., Ginzler, C., Barandun, M., Bebi, P., Bolliger, J., Bollmann, K., Delpouve, N., Gossner, M.M., Graham, C., Krumm, F., Marty, M., Pichon, N., Rigling, A., Rixen, C., 2024. Agricultural practices and biodiversity: Conservation policies for semi-natural grasslands in Europe. Current Biology, 34, R753-R761. https://doi.org/10.1016/j.cub.2024.06.062

Steffan-Dewenter, I., Tscharntke, T., 2002. Insect communities and biotic interactions on fragmented calcareous grasslands—a mini review. Biological conservation, 104(3), 275-284. https://doi.org/10.1016/S0006-3207(01)00192-6

Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A J., Yang, J., Sayol, F., ... Schleuning, M., 2022. AVONET: morphological, ecological and geographical data for all birds. Ecology Letters, 25(3), 581-597. https://doi.org/10.1111/ele.13898

Traba, J., Morales, M.B., 2019. The decline of farmland birds in Spain is strongly associated to the loss of fallowland. Scientific reports, 9(1), 9473.

Valdés-Correcher, E., Mäntylä, E., Barbaro, L., Damestoy, T., Sam, K., Castagneyrol, B., 2022. Following the track: accuracy and reproducibility of predation assessment on artificial caterpillars. Entomologia Experimentalis et Applicata, 170(10), 914-921. https://doi.org/10.1111/eea.13210

Valdés-Correcher, E., van Halder, I., Barbaro, L., Castagneyrol, B., Hampe, A., 2019. Insect herbivory and avian insectivory in novel native oak forests: Divergent effects of stand size and connectivity. Forest Ecology and Management, 445, 146-153. https://doi.org/10.1016/j.foreco.2019.05.018

Vilumets, S., Kaasik, R., Lof, M., Kovács, G., Holland, J., Veromann, E., 2023. Landscape complexity effects on Brassicogethes aeneus abundance and larval parasitism rate: a two-year field study. Scientific Reports, 13(1), 22373. https://doi.org/10.1038/s41598-023-49690-1

WallisDeVries, M.F., Poschlod, P., Willems, J.H., 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biological Conservation, 104(3), 265-273.

Wickham, H., 2016. ggplot2: elegant graphics for data analysis. Springer- Verlag, New York

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875

Wimp, G.M., Ries, L., Lewis, D., Murphy, S.M., 2019. Habitat edge responses of generalist predators are predicted by prey and structural resources. Ecology, 100(6), e02662. https://doi.org/10.1002/ecy.2662

Winkler, K., Fuchs, R., Rounsevell, M., Herold, M., 2021. Global land use changes are four times greater than previously estimated. Nature communications, 12(1), 2501. https://doi.org/10.1038/s41467-021-22702-2

Winqvist, C., Ahnström, J., Bengtsson, J., 2012. Effects of organic farming on biodiversity and ecosystem services: taking landscape complexity into account. Annals of the New York Academy of Sciences, 1249(1), 191-203. https://doi.org/10.1111/j.1749-6632.2011.06413.x

Woodcock, B.A., Pywell, R.F., 2010. Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. Biodiversity and Conservation, 19, 81-95. https://doi.org/10.1007/s10531-009-9703-6

Zvereva, E.L., Castagneyrol, B., Cornelissen, T., Forsman, A., Hernández-Agüero, J. A., Klemola, T., Paolucci, L., Polo, V., Salinas, N., Theron, K.J., Xu, G., Zverev, V., Kozlov, M.V., 2019. Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey. Ecology and Evolution, 9(24), 14273-14285. https://doi.org/10.1002/ece3.5862

Preprint not peer reviewed

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Tables

Table 1. Local and landscape-scale variables used in the analyses.

Variable type	Variable
Local	1. Grassland size 2. Mean caterpillar installation height 3. Grassland management index 4. Invertivore birds' abundance 5. Omnivore birds' abundance
Landscape	1. Connectivity (in 1km and 2km) 2. % of productive AES (in 1km and 2km) 3. % of non-productive AES (in 1km and 2km)
Region	1. Country

Figure captions:

Figure 1: Map of the study regions in Estonia, Germany and Spain.

Figure 2: Predation by country (proportion of caterpillar pair predated). a) Total predation, b) predation by birds, c) predation by arthropods, and d) predation by gastropods. The statistical values of the model are provided in the Table A4, Appendix A.

Figure 3: Predicted relationships between explanatory variables and bird predation (proportion of caterpillar pair predated by birds). a) effect of invertivore birds' abundance on predation; b) effect of the height of exposure on predation; c) effect of connectivity on predation; d) effect of productive AES on predation. Local variables are shown in blue, while landscape variables are shown in yellow.

Figure 4: Effect of local scale variables on arthropods predation (proportion of caterpillar pair predated by arthropods). a) effect of grassland size on predation; b) effect of grassland restoration index on predation; c) effect of height of exposure on predation by country.

Figure 5: Effect of landscape scale variables on arthropods predation (proportion of caterpillar pair predated by arthropods). a) effect of non-productive AES on predation; b) effect of connectivity on predation at different grassland sizes; at 10th percentile (1.1 ha); at the median (2.4 ha); at 90th percentile (7 ha).

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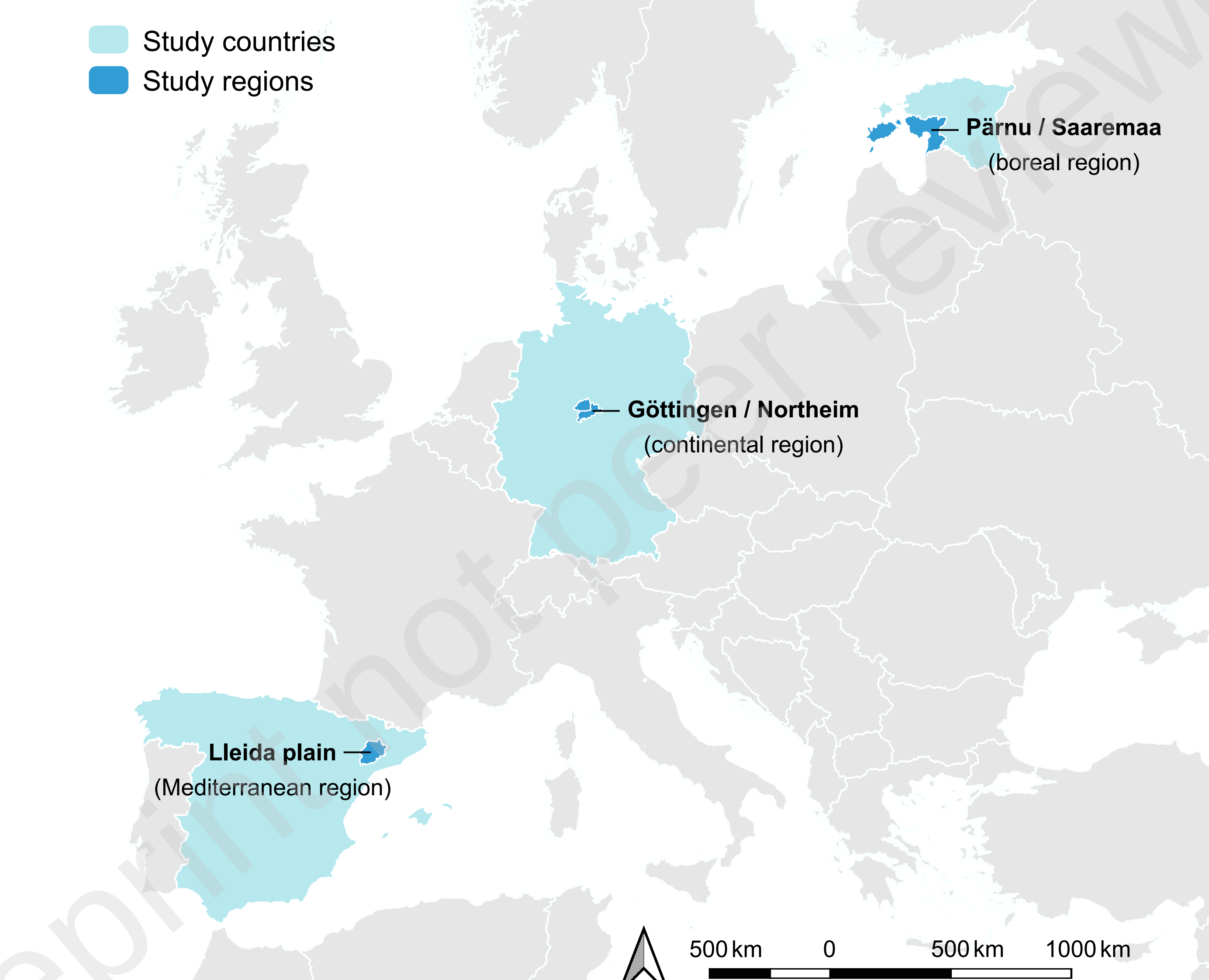

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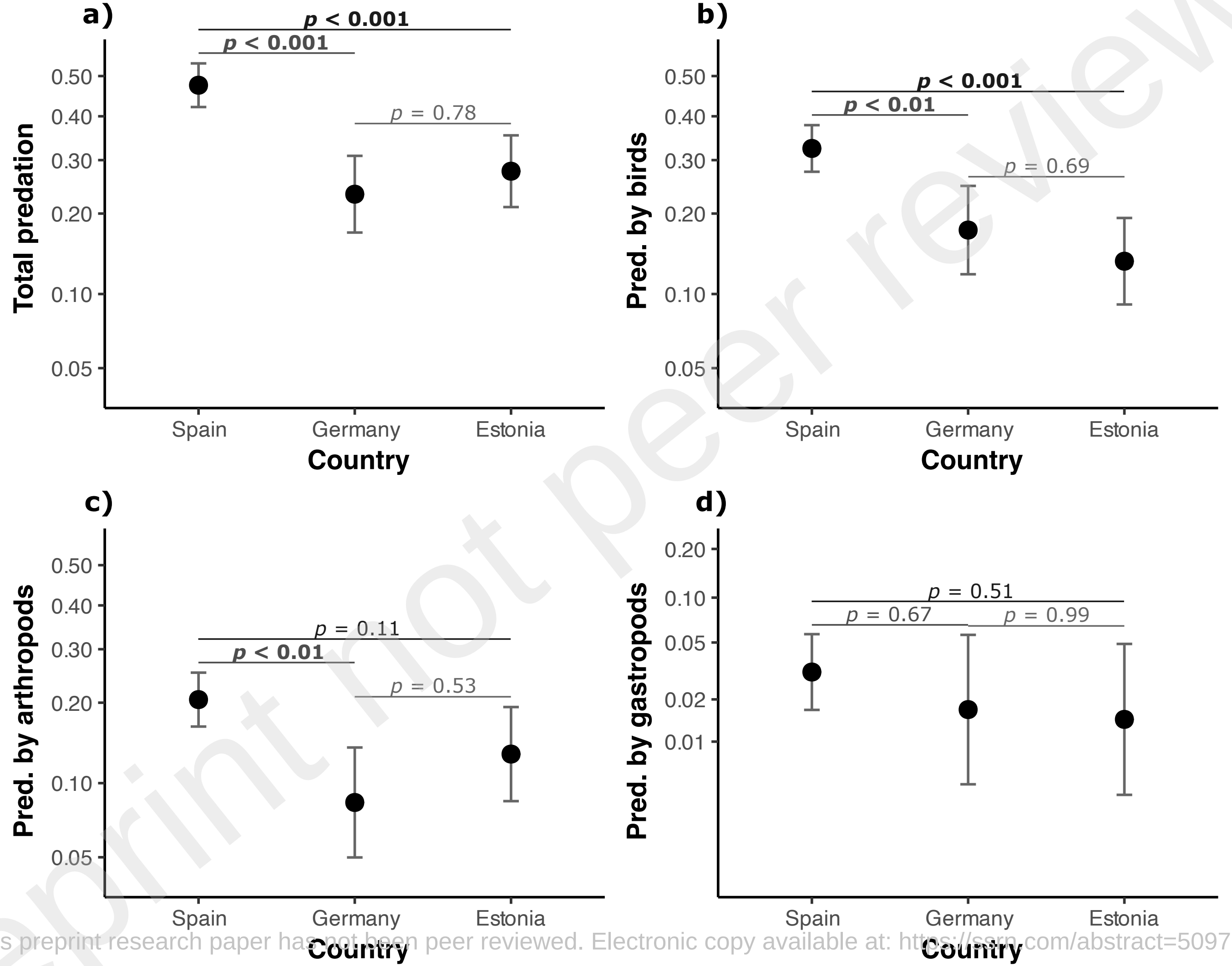

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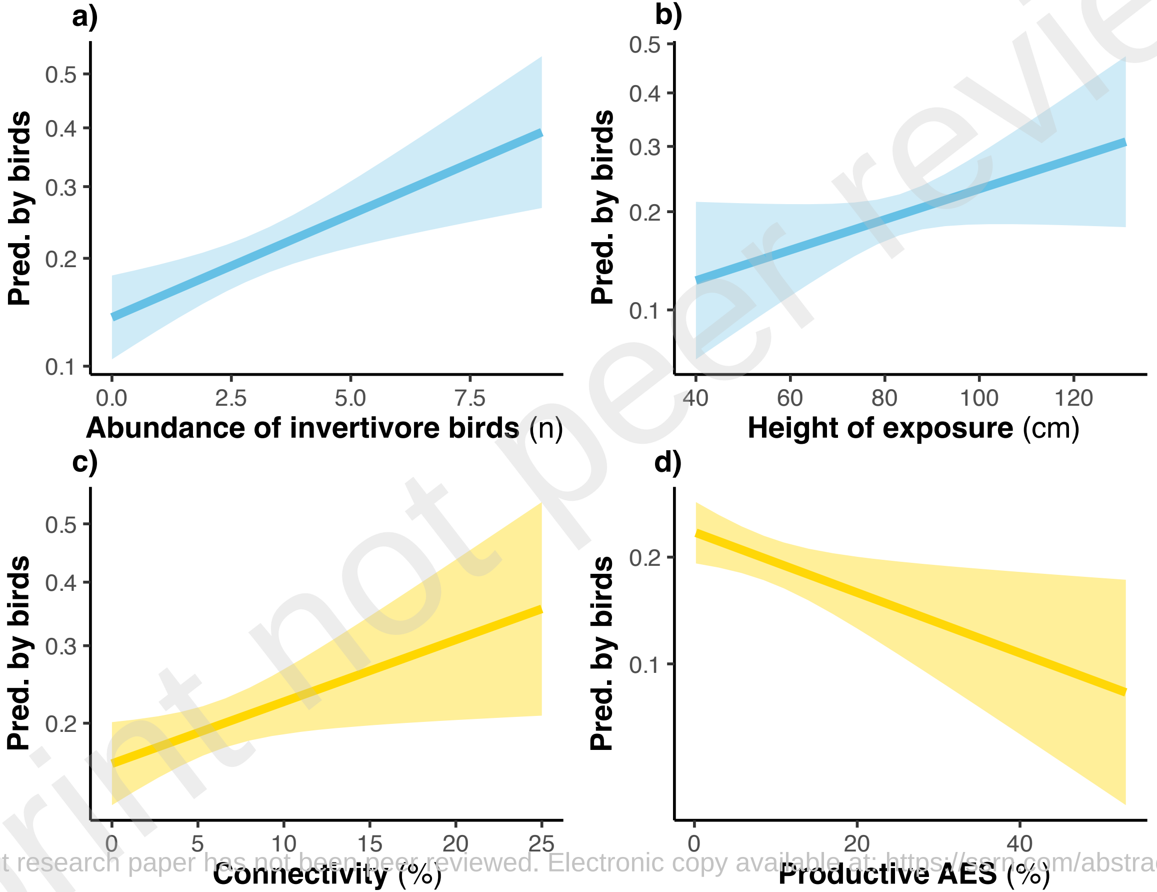

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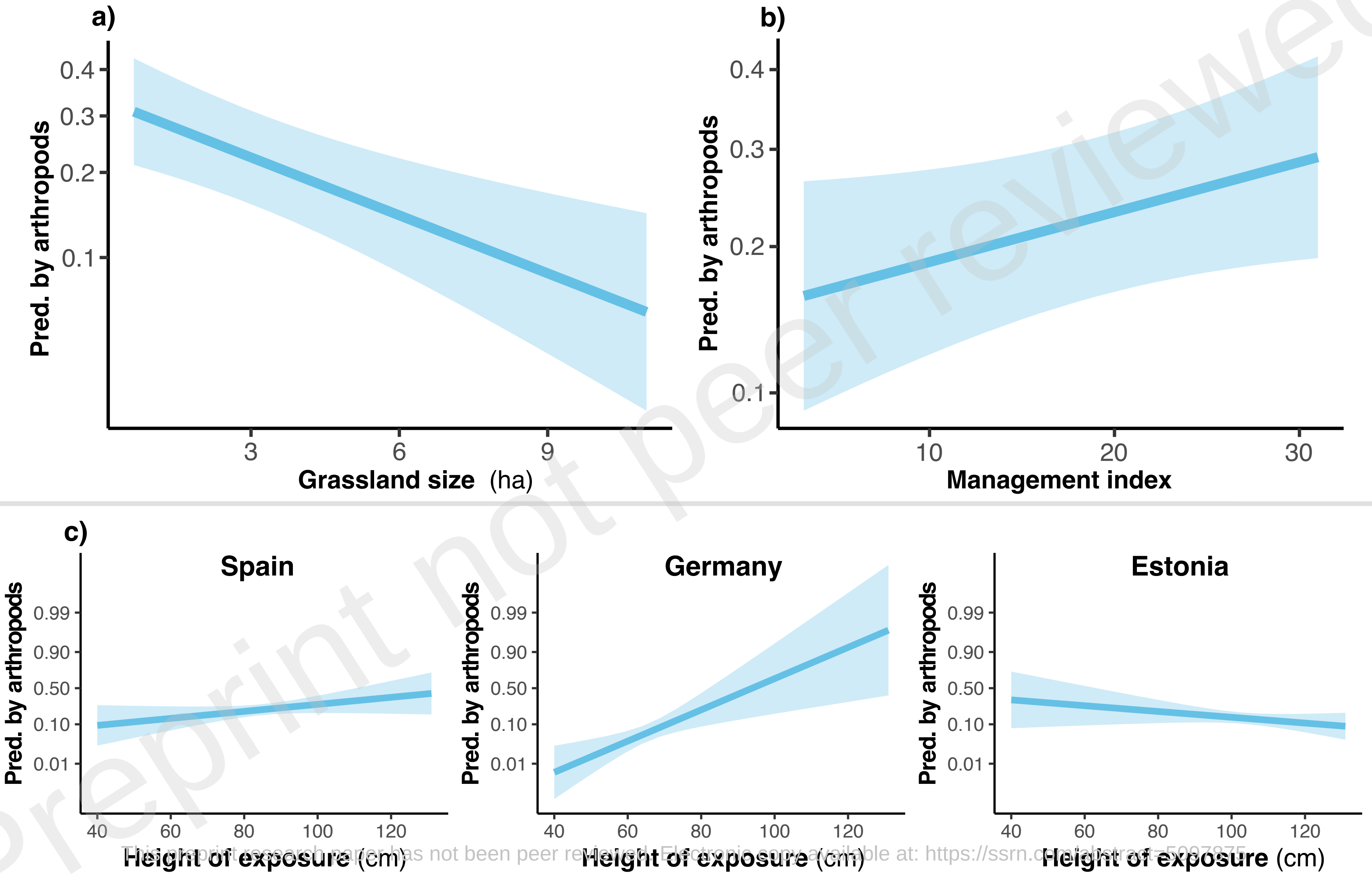
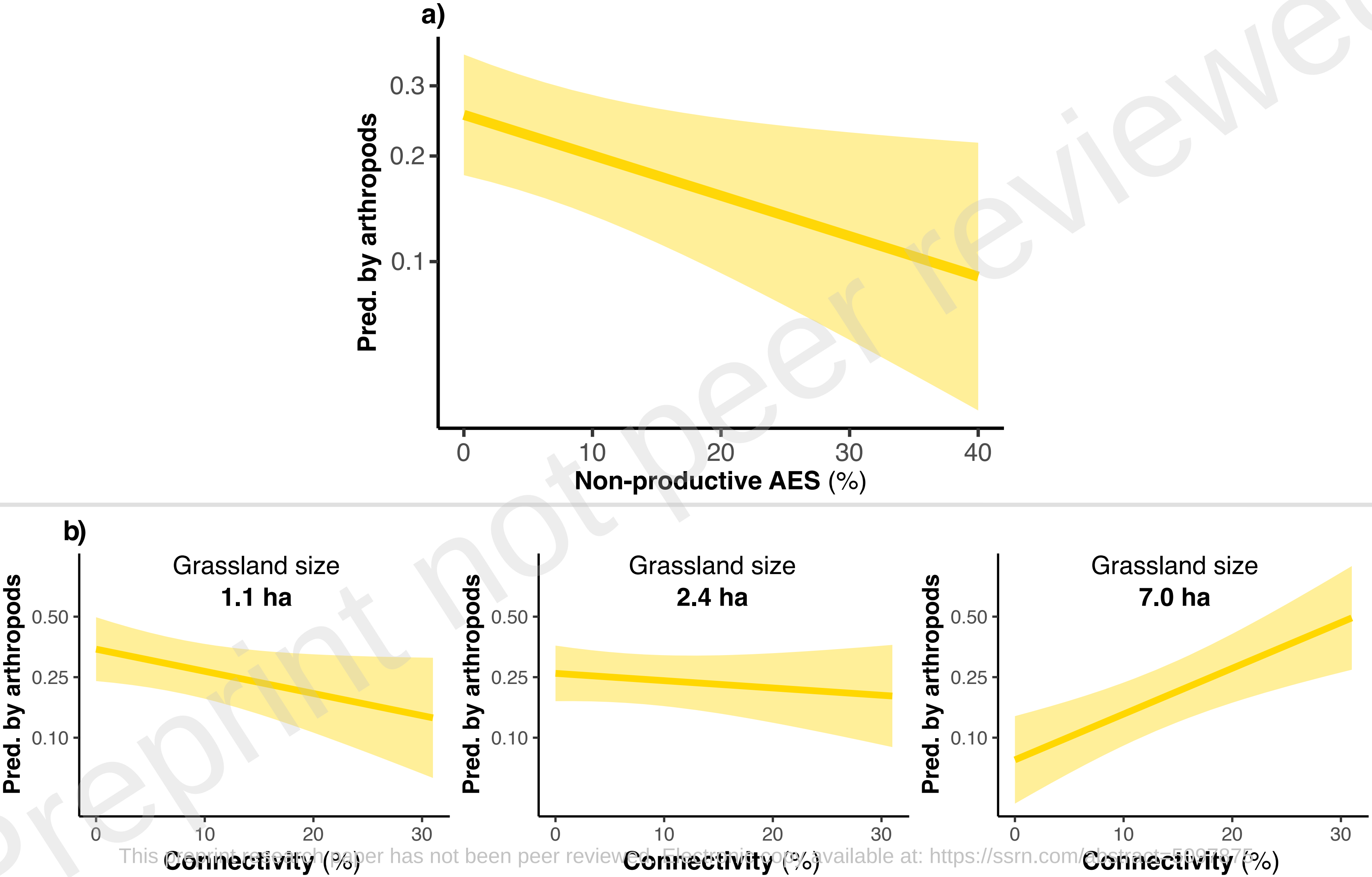


Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875



Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=5097875