Habitat fragmentation weakens the positive relationship between grassland plant richness and above-ground biomass

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Highlights:

1. BEF relationship is moderated by landscape context in fragmented landscapes.
2. Habitat loss and fragmentation per se have inconsistent effects.
3. Habitat loss can weaken the positive BEF relationship.

Abstract:

Anthropogenic habitat fragmentation has been shown to be a major threat to global biodiversity and ecosystem function. However, little is known about how habitat fragmentation alters the relationship between biodiversity and ecosystem function (BEF relationship). Based on 130 landscapes identified using a stratified random sampling in the agro-pastoral ecotone of northern China, we investigated using a structural equation model the effects of habitat fragmentation (including habitat loss and fragmentation per se) on plant richness, above-ground biomass, and the relationship between them in grassland communities. We found that habitat loss decreased plant richness, while fragmentation per se increased plant richness. Fragmentation per se decreased above-ground biomass, while habitat loss had no significant effect on above-ground biomass. Neither habitat loss nor fragmentation per se affected the direction of the positive relationship between plant richness and above-ground biomass. However, habitat loss decreased the magnitude of the positive relationship by reducing the percentage of grassland specialists in the community. These results demonstrate that habitat loss and fragmentation per se have inconsistent effects on biodiversity and ecosystem function, with the BEF relationship being moderated by landscape context. Our findings emphasize that habitat loss rather than fragmentation per se can weaken the positive BEF relationship by decreasing the degree of habitat specialization of the community.

Keywords:

BEF relationship, biodiversity, ecosystem function, fragmentation per se, generalists, habitat loss, moderating effect, specialists.

1 Introduction

Evidence from biodiversity-ecosystem function (BEF hereafter) experiments during the past 30 years generally show positive relationships between biodiversity and productivity, soil carbon storage, decomposition rates, and other ecosystem functions in experimental communities, revealing the importance of biodiversity in maintaining ecosystem functioning (Tilman et al., 2012; van der Plas, 2019). When research expands from experiments to natural systems, however, BEF relationships remain unclear in the natural assembled communities, with significant context dependency (Hagan et al., 2021; van der Plas, 2019). One of the main reasons for these differences

is because the landscape context surrounding natural communities regulates biodiversity and ecosystem function (Gonzalez et al., 2020; Liu et al., 2018). Consideration of the impacts of landscape context on surrounding communities is key to understand complex BEF relationships in natural systems.

Human activities have modified natural ecosystems globally, with habitat fragmentation currently being a typical landscape context (Chase et al., 2020; Maxwell et al., 2016). For example, at least 1.5 billion hectares of natural habitats on Earth have been converted to human-modified land since 2014, breaking apart continuous habitat into smaller and isolated fragments (IPBES, 2019). Habitat fragmentation in natural landscapes consists of two facets: 1) habitat loss, i.e., reducing habitat amount, and 2) fragmentation per se, i.e., breaking apart of habitat such as decreased size of habitat patches, increased number of habitat patches, increased isolation among habitat patches, etc. (Fahrig, 2003; Ibáñez et al., 2014; Wang et al., 2014). Recent studies suggest that habitat loss and fragmentation per se are related to different processes, with inconsistent ecological effects, and should be considered simultaneously to fully understand the ecological consequences of habitat fragmentation (Fahrig et al., 2019; Fletcher et al., 2018; Miller-Rushing et al., 2019).

Habitat fragmentation is often considered the major near-term threat to biodiversity and ecosystem function (Chase et al., 2020; Fletcher Jr et al., 2023; Haddad et al., 2015), while the impact of fragmentation per se remains debated (Miller-Rushing et al., 2019). Habitat fragmentation can also affect BEF relationships. Previous studies have found that the magnitude and direction of BEF relationships vary across fragmented landscapes, including positive, negative, and non-significant relationships (Godbold et al., 2011; Hagan et al., 2021; Rolo et al., 2018; Zirbel et al., 2019). However, few studies have been conducted on how habitat fragmentation regulates BEF relationships (but see, for example, Liu et al., 2018; Wilson et al., 2016). This lack of studies hampers our understanding of complex BEF relationships in fragmented natural ecosystems. In theory, habitat fragmentation can regulate the BEF relationship by altering species composition and interactions regardless of changes in species richness (Liu et al., 2018). However, species in communities are not ecologically equivalent and may respond differently to habitat fragmentation and have different associations with ecosystem function (Devictor et al., 2008;

Wardle and Zackrisson, 2005). Therefore, considering changes in species composition can help to understand how habitat fragmentation regulates BEF relationships.

The degree of habitat specialization is a key ecological characteristic determining responses of species to habitat fragmentation and the slope of BEF relationships (Clavel et al., 2011; Gravel et al., 2011). In fragmented landscapes, species with low levels of habitat specialization (generalists) can use resources from different land covers, including focal habitat and non-habitat matrix, and thus are not sensitive to habitat fragmentation (Matthews et al., 2014). In contrast, species with high levels of habitat specialization (specialists) depend highly on resources in specific habitats, and thus are vulnerable to adverse effects from habitat fragmentation (Matthews et al., 2014). Meanwhile, specialists in communities are often highly productive and competitive, which are closely associated with ecosystem function, whereas generalists are less productive and competitive, which are redundant for ecosystem function (Dehling et al., 2021; Gravel et al., 2011; Mello et al., 2015). Therefore, habitat fragmentation is often considered to decrease the degree of habitat specialization (the replacement of specialists in communities by generalists), possibly resulting in functional homogenization of communities and reduced BEF relationships (Clavel et al., 2011; Matthews, 2021). However, few studies have evaluated this process in fragmented landscapes.

Currently, research on habitat fragmentation focuses primarily on forest ecosystems (Fardila et al., 2017; Haddad et al., 2015). Grasslands have received considerably less attention, despite being the largest terrestrial ecosystem type, and suffering severe fragmentation due to human activities, such as agricultural reclamation and urbanization (Fardila et al., 2017). The agro-pastoral ecotone of northern China is a typical anthropogenically fragmented grassland landscape caused by historical agricultural reclamation, especially in the late Qing Dynasty (about 1840–1912). Due to land policy reforms, the region has experienced a rapid expansion of farmland since the 1960s, converting continuous natural grasslands into smaller and isolated fragments (Wu et al., 2015; Yang et al., 2020). Habitat fragmentation has reduced plant diversity and ecosystem function in these grassland fragments (Yan et al., 2022; Yan et al., 2023; Yang et al., 2020). However, whether habitat fragmentation affects the relationship between plant diversity and ecosystem function is still unclear.

Based on 130 landscapes with different fragmentation levels in the agro-pastoral ecotone of northern China, we investigated how habitat fragmentation (including habitat loss and fragmentation per se) regulates the relationship between grassland plant diversity and above-ground productivity in the community. Specifically, we aimed to evaluate whether habitat fragmentation would weaken the positive relationship between grassland plant diversity and above-ground productivity by reducing the habitat specialization of the community.

2 Materials and methods

2.1 Study area

Our study area is in the agro-pastoral ecotone of northern China, the Tabu River Basin in Siziwang Banner, Inner Mongolia Autonomous Region. The mean annual temperature ranges from 1.5 to 5.0 □, and the mean annual precipitation ranges from 225 to 322 mm. The type of soil is light chestnut soil. This area is a typical fragmented grassland landscape caused by agricultural intensification. Grassland is the dominant natural habitat type in this area, accounting for about 40.8 % of the total area, with the dominant plant species being *Stipa krylovii* and S. *breviflora*. Farmland is the dominant matrix type in this area, accounting for about 30.6 % of the total area, with the main crops grown are potatoes and maize. Further background information about the study area is described in our previous papers (Yan et al., 2022; Yan et al., 2023; Yan et al., 2021; Zhang et al., 2021).

2.2 Sampling landscape selection

We quantified landscape-scale habitat fragmentation in the study area to determine the spatial gradient of habitat fragmentation (including habitat loss and fragmentation per se), then established the sampling landscapes. Grassland was defined as the focal habitat. Habitat amount was represented by the percentage of grassland cover in the landscape. Habitat loss was represented by non-grassland cover in the landscape. Fragmentation per se was estimated using four landscape indices, reflecting different landscape-scale fragmentation processes (Fahrig, 2003;

Fahrig, 2017): (1) mean patch area metric, representing a decrease in grassland patches area in the landscape; (2) mean nearest-neighbor distance metric, representing an increase in the isolation of grassland patches in the landscape; (3) patch density metric, representing an increase in the number of grassland patches in the landscape; and (4) edge density metric, representing an increase in the grassland edges in the landscape. Given that habitat amount (or habitat loss) and fragmentation per se are typically highly correlated in natural landscapes, it is hard to disentangle their relative effects (Fahrig, 2017; Smith et al., 2009). We therefore used stratified sampling to select sampling landscapes across the relative independent spatial gradient of habitat amount and fragmentation per se, which can reduce collinearity between them (Pasher et al., 2013; Reynolds et al., 2018).

To do so, we first used the moving window method (window size: 500-m radius buffer) to quantify grassland amount and the four landscape indices surrounding all grassland cells. The 500-m radius buffer was used because our previous studies showed this buffer includes the optimal scale of spatial processes influencing grassland plant diversity in this region (Yan et al., 2022; Yan et al., 2023; Zhang et al., 2021). Second, we derived the first principal component (PC1) of the four landscape indices as a single fragmentation per se index (Hertzog et al., 2019; Rolo et al., 2018). This index was positively correlated with patch density, edge density, mean nearest-neighbor distance metric, and negatively with mean patch area (Appendix Figure A1 and Table A1). Based on the quartiles of grassland amount and PC1 of the four landscape indices, we ranked these grassland cells into nine types: high-high, high-moderate, high-low, moderate-high, moderate-moderate, moderate-low, low-high, low-moderate, low-low grassland amount and fragmentation per se (Appendix Figure A2). Given landscapes with a high grassland amount and high fragmentation are scarce in this region (Appendix Figure A2), we did not consider this type of landscape. Finally, we selected at least 20 landscapes using stratified sampling from each of the remaining eight grassland types as sites for field surveys.

The land-cover data used to quantify grassland fragmentation was obtained via supervised classification on a cloud-free Landsat 8 TOA composite image (30-m resolution) from 2019 (Yan et al., 2022). We used the random forest classifier in the Google Earth Engine platform (Gorelick et al., 2017) for the supervised classification. The moving window analysis and all landscape

metric calculations were performed in FRAGSTATS v4.2.1 based on the eight-cells neighborhood rule (McGarigal et al., 2012). The principal component analysis was performed in the R programming language v. 4.0.3 (R Development Core Team, 2020). Stratified sampling was conducted in ArcGIS v10.3.

2.3 Biodiversity and ecosystem function surveys

Based on the landscapes selected above, we established 130 sites (30 m * 30 m) between late July to mid-August 2020 in the Tabu River Basin in Siziwang Banner, Inner Mongolia Autonomous Region (Figure 1). To prevent overlapping landscapes and potential spatial autocorrelation, the shortest distance between each site was at least 1000 m. The type of habitat of the selected sites was grasslands with regional vegetation characteristics. Each site showed no signs of having been reclaimed. In the center of each site, we surveyed grassland vascular plant diversity and above-ground productivity in 1 m * 1 m plots set within 10 m * 10 m topographically flat areas. Plant diversity was obtained by recording the number of vascular plant species in each plot. The above-ground productivity was obtained by harvesting the above-ground biomass of the plants in each plot and drying biomass at 65 °C to a constant weight.

As grassland is the dominant habitat type in the fragmented landscape and farmland is the dominant matrix type, the specialists and generalists in this study were grouped as grassland specialists, i.e., species that occur only in grassland, and weeds, i.e., species that occur in both grassland and farmland. The classification of grassland specialists and weeds in this study was based on our experience with plant surveys in this region, the List of Main Crop Weeds in China, and available information in the Flora of China (http://www.iplant.cn/frps).

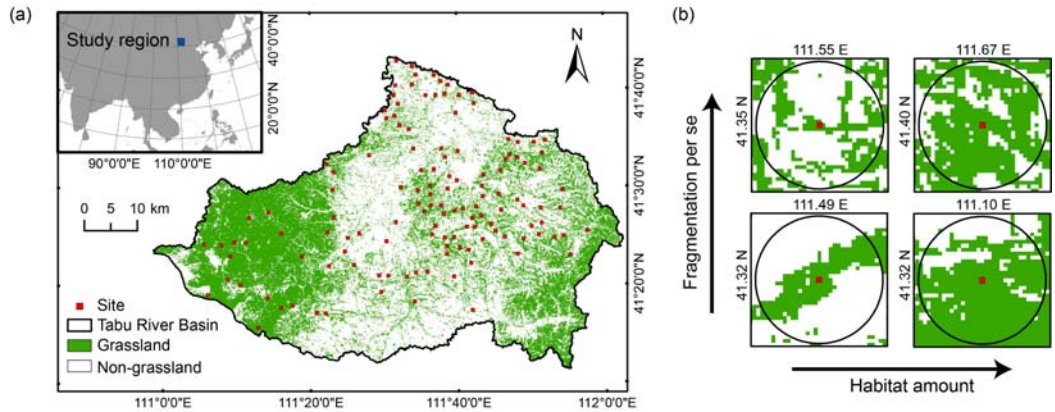

Figure 1. Map of study area in the Tabu River Basin, Inner Mongolia Autonomous Region, northern China. (a) Location of the 130 survey sites in the study area. (b) Examples of four survey sites with varying levels of habitat loss and fragmentation per se shown with a 500-m radius buffer.

2.4 Data analysis

For each site, we used data from three 1 m * 1 m plots to calculate the mean richness of vascular plant, representing the vascular plant diversity, and mean above-ground biomass of vascular plants, representing the above-ground productivity. The mean vascular plant richness and the mean above-ground biomass of vascular plants were assessed to be normally distributed by a Shapiro-Wilk normality test. The degree of habitat specialization was represented the percentage of grassland specialists in the community. Habitat loss was represented by the percentage of non-grassland cover in the landscape and fragmentation per se was represented by the first principal component of the four landscape indices (mean grassland patch area, mean nearest-neighbor distance among grassland patch, grassland patch density, grassland patch edge).

First, to investigate the impact of habitat fragmentation on grassland vascular plant diversity, we used a linear regression model to estimate the effects of habitat loss and fragmentation per se on grassland plant richness (including grassland specialist richness and weed richness).

Second, to investigate the relative importance of habitat fragmentation and grassland vascular plant diversity on above-ground productivity, we used the multi-model averaging method based on the Akaike information criterion corrected for a small sample size (AICc) (Harrison et al., 2018).

We first constructed linear regression models, including the response variable (above-ground biomass) and all combinations of the predictor variables (habitat loss, fragmentation per se, grassland specialist richness, and weed richness). The models with the lowest AICc value and a difference of less than two ΔAICc from the lowest AICc value were selected as optimal models. We then calculated the model-averaged standardized parameter estimate based on the optimal models as the relative effect of each influencing factor on above-ground biomass (Harrison et al., 2018). Before the analysis, we calculated the variance inflation factors (VIF) for each predictor variable to assess multicollinearity. The VIF of all explanatory variables was less than three (Appendix Table A2), suggesting no significant multicollinearity in the analysis (Carrara et al., 2015; Dormann et al., 2013).

Finally, we used the piecewise structural equation model to investigate how habitat fragmentation regulates the relationship between grassland plant diversity and above-ground productivity. We first constructed a hypothetical conceptual model (Figure 2). Based on previous studies, we hypothesized that habitat loss and fragmentation per se could decrease above-ground biomass directly and decrease plant richness indirectly (Allan et al., 2015; Haddad et al., 2015; Rolo et al., 2018). We also hypothesized that habitat loss and fragmentation per se could both decrease the impact of plant richness on above-ground biomass by decreasing the percentage of grassland specialists in the community (Clavel et al., 2011; Gravel et al., 2011; Liu et al., 2018). We included the interaction between the percentage of grassland specialists and the plant richness as predictor variables to quantify the moderating effect of the percentage of grassland specialists for the impact of plant richness on above-ground biomass. We tested the hypothetical conceptual model using a piecewise structural equation model (Lefcheck, 2016). The global fit of the model was evaluated using the Fisher's C statistic, and the hypothetical pathways were evaluated by standardized path coefficients. In addition, we used linear regression models to evaluate the relationship between plant richness and above-ground biomass at low, moderate, and high levels of habitat loss and fragmentation per se, respectively.

All data analyses were performed in the R programming language v. 4.0.3 (R Development Core Team, 2020) with the following functions and packages. The linear regression model and the Shapiro-Wilk normality test were conducted with 'lm' and 'shapiro.test' functions of the stats

package (R Development Core Team, 2020). The multi-model averaging were conducted with the 'dredge' and 'model.avg' functions of the MuMIn package (Bartoń, 2020). The VIF was calculated with the 'vif' function of the car package (Fox and Weisberg, 2019). The piecewise structural equation model was conducted and tested with the 'psem' function of the piecewiseSEM package (Lefcheck, 2016).

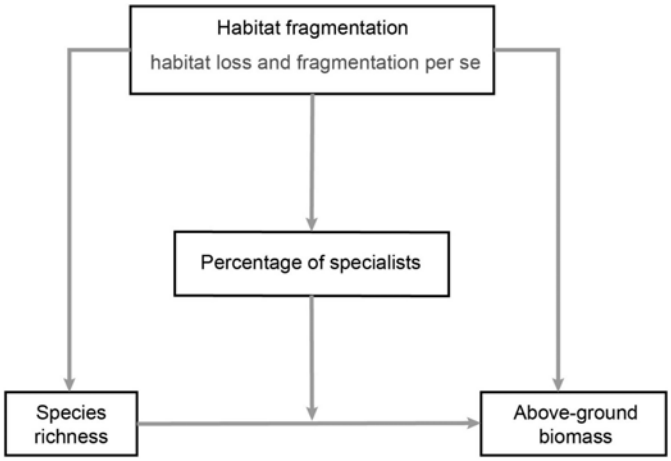

Figure 2. Hypothetical model of habitat fragmentation that alters the relationship between grassland plant diversity and above-ground biomass by affecting the percentage of grassland specialists in the community in the Tabu River Basin, a typical agro-pastoral ecotone of northern China. Arrows represent the hypothesized paths among variables. See the main text for a description of arrow directions.

3 Results

3.1 Effect of habitat fragmentation on grassland plant richness

Habitat loss had a significant negative effect on overall species richness ($p < 0.05$) and grassland specialist richness ($p < 0.01$), but a significant positive effect on weed richness ($p < 0.01$, Figure 3a). Fragmentation per se had no significant effect on overall species richness and grassland specialist richness, but a significant positive effect on weed richness ($p < 0.01$, Figure 3b).

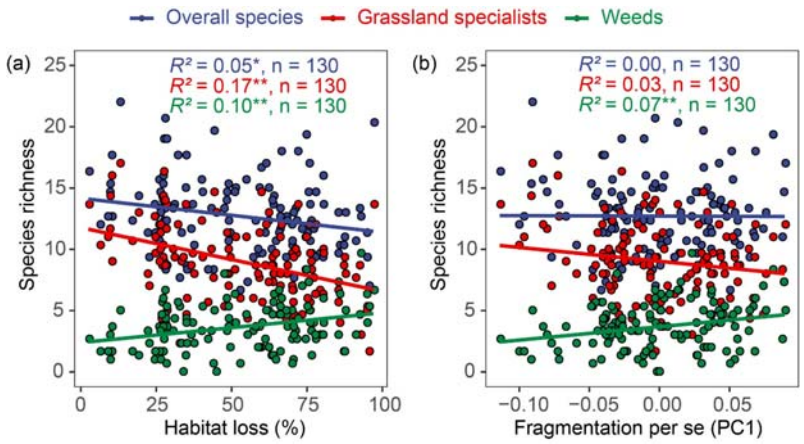

Figure 3. Relationship between habitat fragmentation and grassland plant richness in the Tabu River Basin, a typical agro-pastoral ecotone of northern China. The R^2 values in the figure are from linear regression models. The *n* in the figure is the number of surveying sites used in the linear regression models. * and ** represent significance at the 0.05 and 0.01 levels, respectively.

3.2 The relative impacts of habitat fragmentation and grassland plant richness on above-ground biomass

Habitat loss had no significant effect on above-ground biomass, and fragmentation per se had a significant negative effect on above-ground biomass ($p < 0.05$). Grassland specialist richness and weed richness had a significant positive effect on above-ground biomass ($p < 0.01$). The effects of grassland specialist richness and weed richness on above-ground biomass were stronger than fragmentation per se (Figure 4).

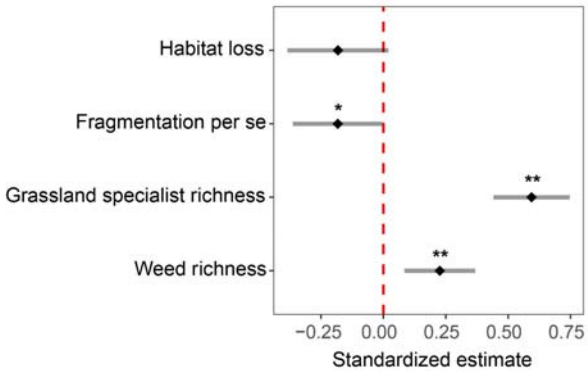

Figure 4. Standardized parameter estimates and 95% confidence intervals for habitat fragmentation and plant richness affecting above-ground biomass in the Tabu River Basin, a

typical agro-pastoral ecotone of northern China. Standardized estimates and 95% confidence intervals are calculated by the multi-model averaging method. * and ** represent significance at the 0.05 and 0.01 levels, respectively.

3.3 The impact of habitat fragmentation on the relationship between grassland plant richness and above-ground biomass

The Fisher's C statistic indicated that the piecewise structural equation model fitted the data well (*Fisher's C*=5.5, *P*-value > 0.05, Figure 5). Habitat loss was shown by the piecewise structural equation model to have no direct effect on above-ground biomass, and an indirect negative effect on above-ground biomass through decreasing overall species richness. Fragmentation per se had a direct negative effect on above-ground biomass and an indirect positive effect on above-ground biomass through increasing overall species richness.

Meanwhile, the piecewise structural equation model showed that the percentage of grassland specialists increased the effect of overall species richness on above-ground biomass (Figure 5). Habitat loss decreased the effect of overall species richness on above-ground biomass by decreasing the percentage of grassland specialists. Fragmentation per se had no significant effect on the percentage of grassland specialists.

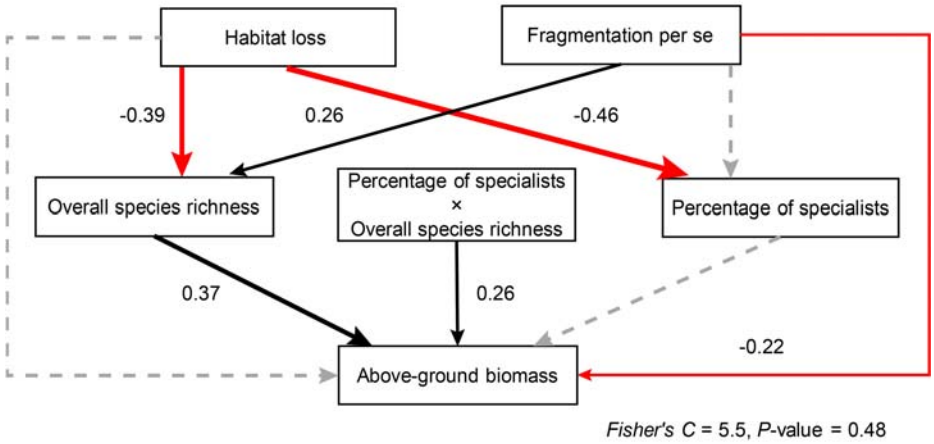

Figure 5. Results from piecewise structural equation model with hypothesized paths showing how habitat fragmentation alters the relationship between grassland plant richness and above-ground biomass in the Tabu River Basin, a typical agro-pastoral ecotone of northern China.

The widths of arrows are proportional to the standardized path coefficients. Black and red solid arrows represent the positive and negative effects, respectively. Black solid and grey dashed arrows represent the significant and nonsignificant effects at the 0.05 level, respectively. The Fisher's C and P-values are from the piecewise structural equation model.

Results of the linear regression showed that there was a positive relationship between plant richness and above-ground biomass at low, moderate, and high levels of habitat loss (Figure 6). The positive relationship was strongest at low levels of habitat loss and weakest at high levels of habitat loss.

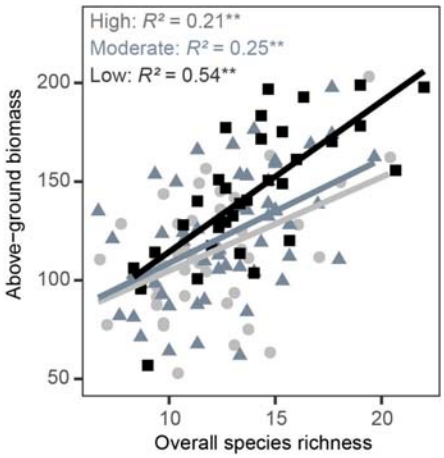

Figure 6. Relationships between grassland plant richness and above-ground biomass at low, moderate, and high levels of habitat loss from 130 landscapes in the Tabu River Basin, a typical agro-pastoral ecotone of northern China. The R^2 values in the figure are from linear regression models. ** represent significance at the 0.01 level.

4 Discussion

4.1 Habitat loss and fragmentation per se had inconsistent effects on grassland plant diversity and ecosystem function

Previous studies investigating the influence of habitat fragmentation on biodiversity and ecosystem function mainly conducted at the patch level generally indicate the negative effects of

habitat fragmentation on multitrophic biodiversity and multiple ecosystem function (Haddad et al., 2015; Hertzog et al., 2019; Rolo et al., 2018). However, habitat fragmentation is often considered a landscape-wide phenomenon ideally to be understood at the landscape level (Fahrig, 2017; McGarigal and Cushman, 2002). We evaluated the effects of two facets of habitat fragmentation at the landscape scale (habitat loss and fragmentation per se) on grassland plant diversity and above-ground productivity in the agro-pastoral ecotone of northern China, with our results showing the effects of these two facets to not be consistent.

Consistent with previous studies, we found habitat loss significantly reduced grassland plant diversity, suggesting that habitat loss is a major threat to the biodiversity conservation of fragmented landscapes in this region (Chase et al., 2020; Haddad et al., 2015; Ibáñez et al., 2014). While for fragmentation per se, we found a positive effect on grassland plant diversity, in accordance with some recent evidence the effects of fragmentation per se on biodiversity are more likely positive than negative (Gestich et al., 2022; Palmeirim et al., 2019; Riva and Fahrig, 2023). This is mainly because when the amount of habitat in the landscape is not reduced fragmentation per se may promote biodiversity through increasing habitat diversity, increasing landscape connectivity, reducing competition, and other mechanisms (Fahrig, 2017). Our study suggests that biodiversity conservation strategies for fragmented landscapes should consider optimizing the habitat configuration in the landscape in addition to preventing habitat loss, such as increasing the number of habitat patches (Arroyo-Rodríguez et al., 2020).

Our results showed for a metric of ecosystem function that fragmentation per se significantly decreased above-ground productivity, whereas habitat loss did not. A possible reason for this finding is fragmentation per se could directly alter environmental factors affecting ecosystem function through enhanced edge effects (Laurance et al., 2011; Smith et al., 2018). The negative effect of fragmentation per se on above-ground productivity in our study may be due to increased drought severity caused by edge effects (Brookshire and Weaver, 2015). Previous studies showed edge effects could lead to ecosystem drought by causing greater desiccation and evapotranspiration rate, which is a major factor limiting productivity in grassland ecosystems (Smith et al., 2018; Tuff et al., 2016). Our study, generally, suggests habitat loss and fragmentation per se have inconsistent effects on plant diversity and ecosystem function in fragmented

landscapes. Future studies should simultaneously consider habitat loss and fragmentation per se to understand the consequences of habitat fragmentation.

4.2 Habitat fragmentation did not change the direction of the positive relationship between plant diversity and ecosystem function, but weakened the magnitude of the relationship

Understanding the direction and magnitude of BEF relationships in fragmented landscapes is essential to understand the importance of biodiversity for ecosystem function in the changing world (Gonzalez et al., 2020; van der Plas, 2019). In naturally assembled communities, ecosystem functions may be dominated by complex environmental factors and landscape context, showing a weak or even negative correlation with biodiversity (Grace et al., 2007; Hagan et al., 2021; Zirbel et al., 2019). Our study found grassland plant diversity showed a significant positive correlation with aboveground productivity and its relative importance was stronger than that of habitat fragmentation. This result is consistent with findings from BEF experiments (Fanin et al., 2018; Hong et al., 2022), indicating habitat fragmentation did not change the direction of the positive BEF relationship in this region. Thus, our study shows grassland plant diversity has an important role in maintaining grassland ecosystem functions in the fragmented landscapes of the agro-pastoral ecotone of northern China.

Although habitat fragmentation did not change the direction of the positive BEF relationship, we found it could weaken the magnitude of the relationship through habitat loss. This is consistent with predictions of theoretical models of habitat fragmentation affecting the relationship between biodiversity and ecosystem function (Clavel et al., 2011; Liu et al., 2018). Our finding suggests habitat loss could reduce the importance of plant diversity to ecosystem function in fragmented landscapes of the agro-pastoral ecotone of northern China. However, a recent study by Hertzog et al. (2019) on temperate forest ecosystems found that habitat fragmentation could strengthen the positive relationship between plant diversity and ecosystem multifunctionality. This inconsistency can be explained by trade-offs between different ecosystem functions that may differ in their response to habitat fragmentation (Banks-Leite et al., 2020). Therefore, future studies are needed

to focus on multiple ecosystem functions and consider their potential trade-offs.

We found habitat loss weakened the positive BEF relationship by decreasing the percentage of specialists in grassland communities, as specialists were more vulnerable to the negative effect of habitat loss and more associated with ecosystem function than generalists. These findings indicate reducing the degree of habitat specialization may be the mechanism of habitat fragmentation altering the BEF relationship in the fragmented landscapes of this region (Clavel et al., 2011; Gravel et al., 2011). Thus, our study provides evidence that habitat fragmentation could decrease the degree of habitat specialization by leading to the replacement of specialists by generalists in the community, thus weakening the BEF relationship (Clavel et al., 2011). Our findings suggest further expansion of farmland in the agro-pastoral ecotone of northern China would decrease the grassland plant diversity and its importance to ecosystem function.

5 Conclusions

Our study investigated the effects of two aspects of habitat fragmentation (habitat loss and fragmentation per se) on grassland plant diversity, above-ground productivity, and their relationships in the agro-pastoral ecotone of northern China. We found habitat loss and fragmentation per se had inconsistent effects. Habitat loss decreased grassland plant diversity, while fragmentation per se increased grassland plant diversity. Habitat loss did not affect above-ground biomass, while fragmentation per se decreased above-ground biomass. We also found habitat fragmentation did not change the direction of the positive relationship between grassland plant diversity and above-ground biomass, but weakened the magnitude of the relationship by decreasing the habitat specialization of the community. Our study suggests biodiversity conservation in fragmented landscapes should focus on preventing habitat loss, which decreases plant diversity and its importance to ecosystem function.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA ACCESSIBILITY STATEMENT

We have unloaded the data as supplementary materials. If the manuscript is accepted, we will upload the data to a publicly accessible digital repository.

AUTHORS' CONTRIBUTIONS

Q.Z. and Y.Z. conceived the research; Y.Z., S.J., and Q.Z. contributed to the writing of the manuscript; Y.Z. and S.J. contributed to data compilation and analysis; Y.Z. and Q.Z. contributed to the fieldwork.

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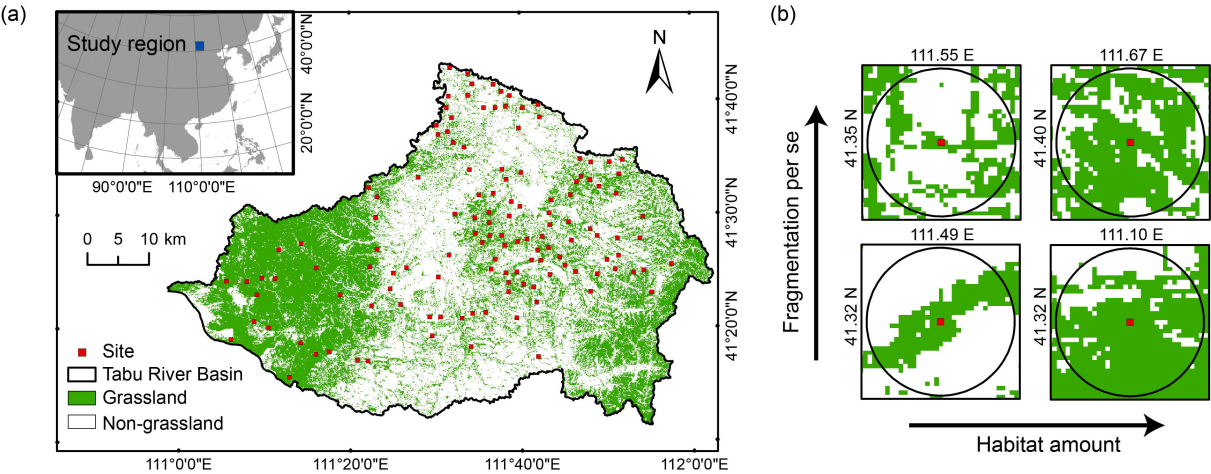
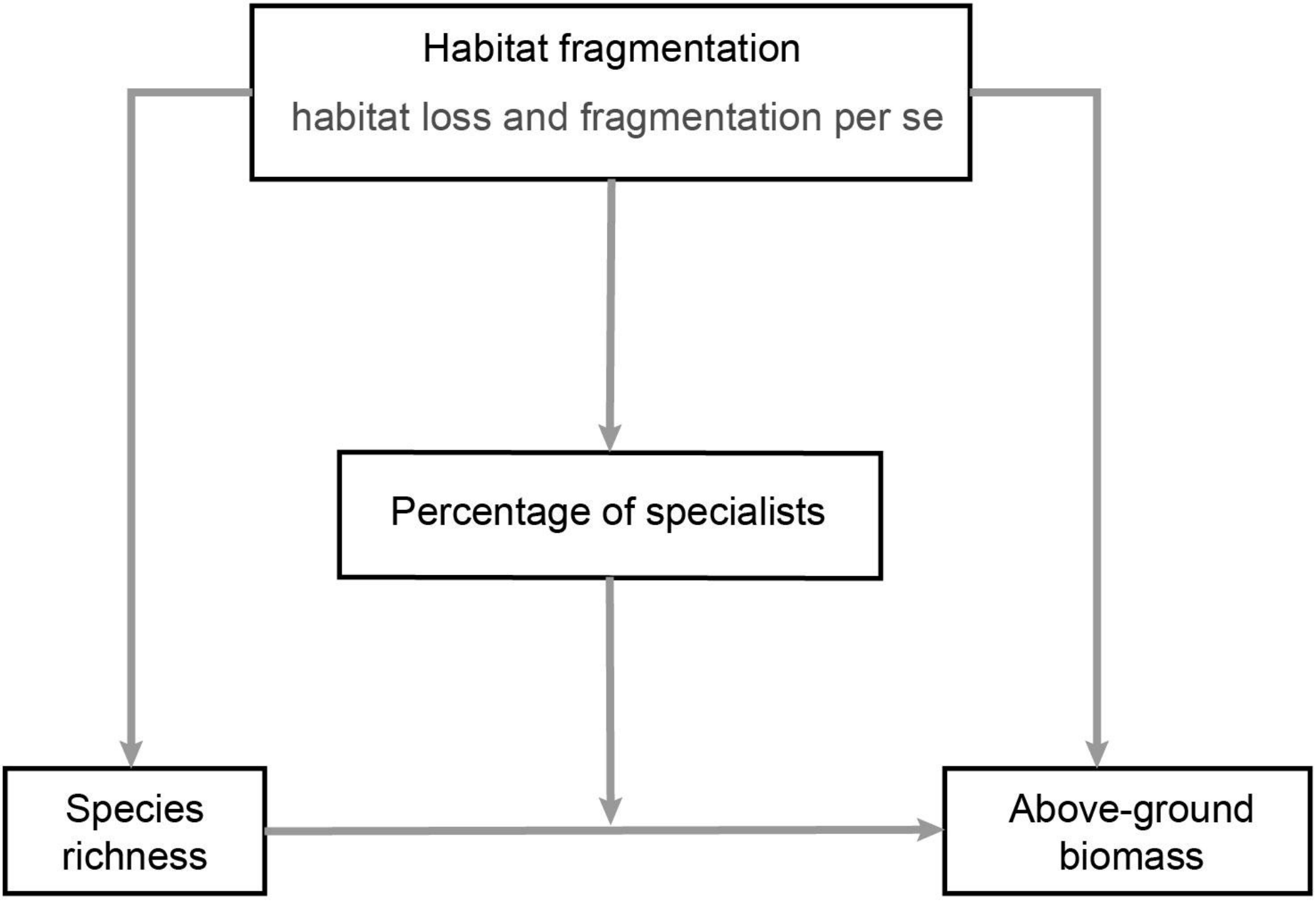
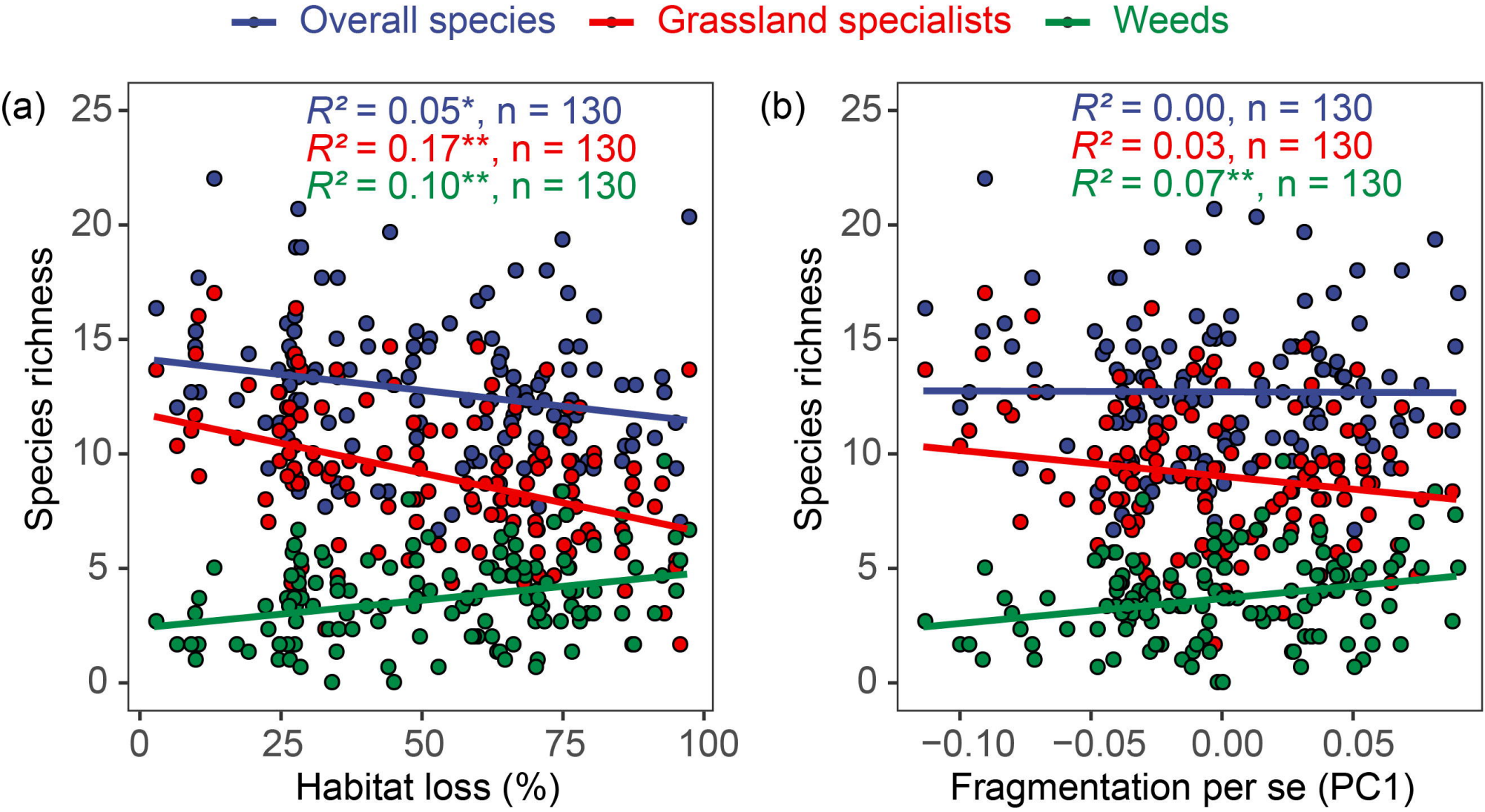
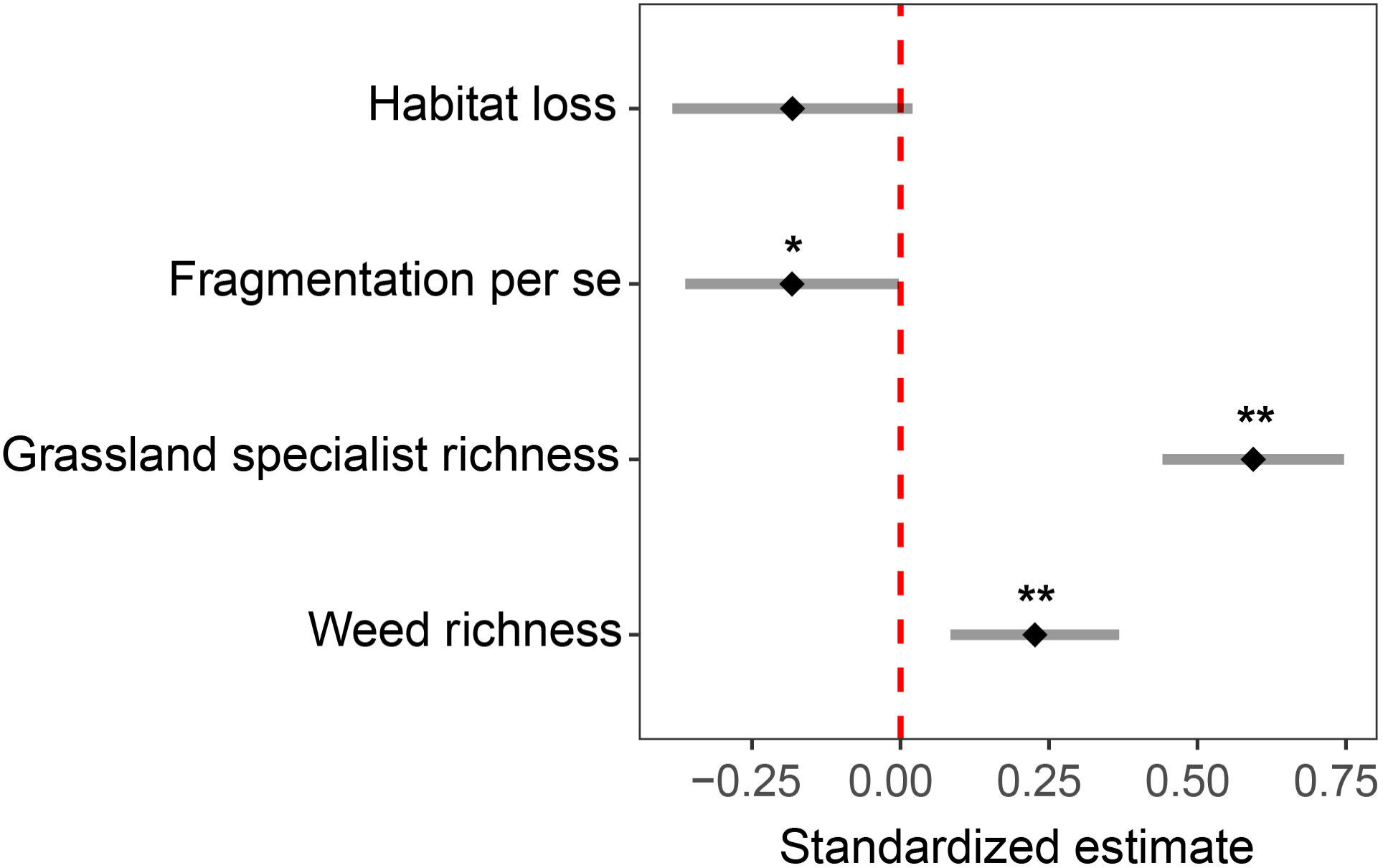
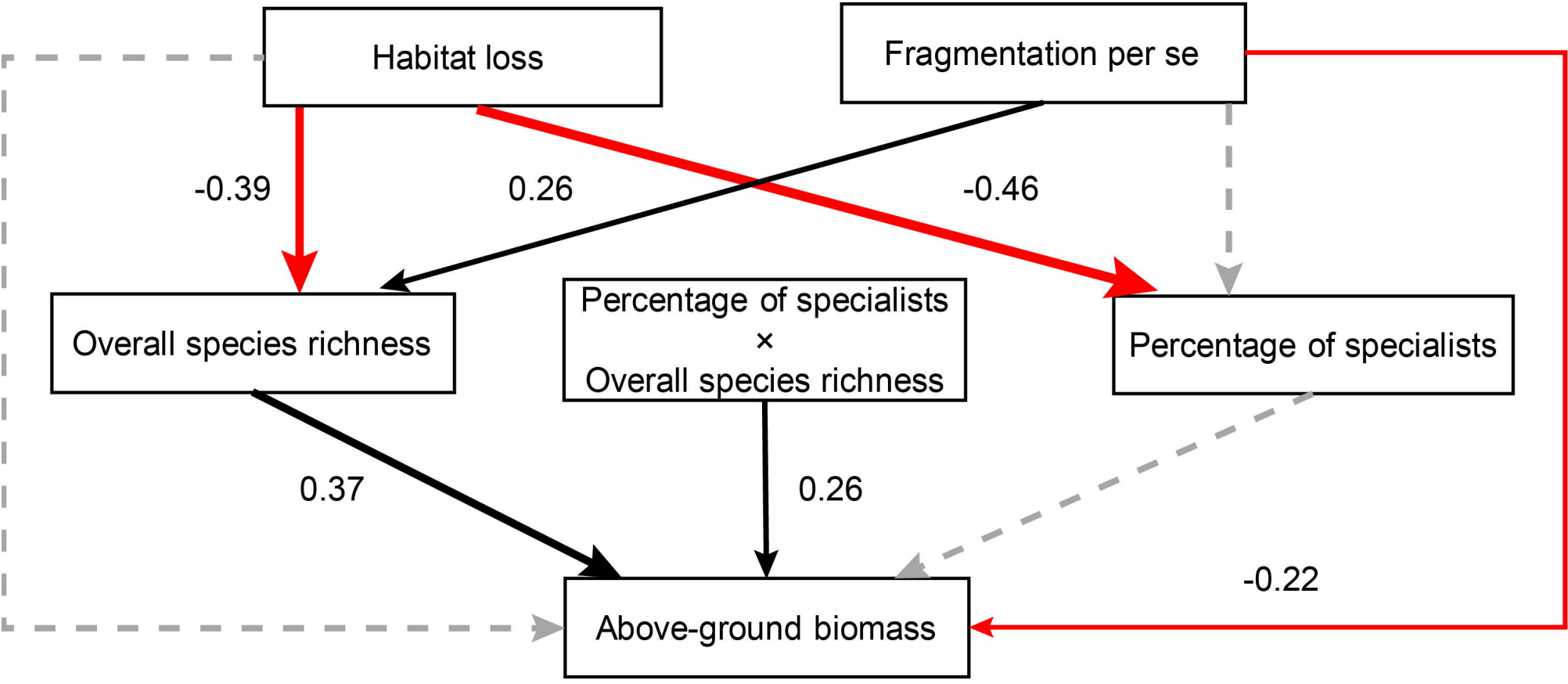

(a)
Study region
90°0'0"E
110°0'0"E
40°0'0"N
20°0'0"N
N
0 5 10 km
Site
Tabu River Basin
Grassland
Non-grassland
41°40'0"N
41°30'0"N
41°20'0"N
111°0'0"E
111°20'0"E
111°40'0"E
112°0'0"E
(b)
111.55 E
111.67 E
111.49 E
111.10 E
41.35 N
41.40 N
41.32 N
41.32 N
Fragmentation per se
Habitat amount

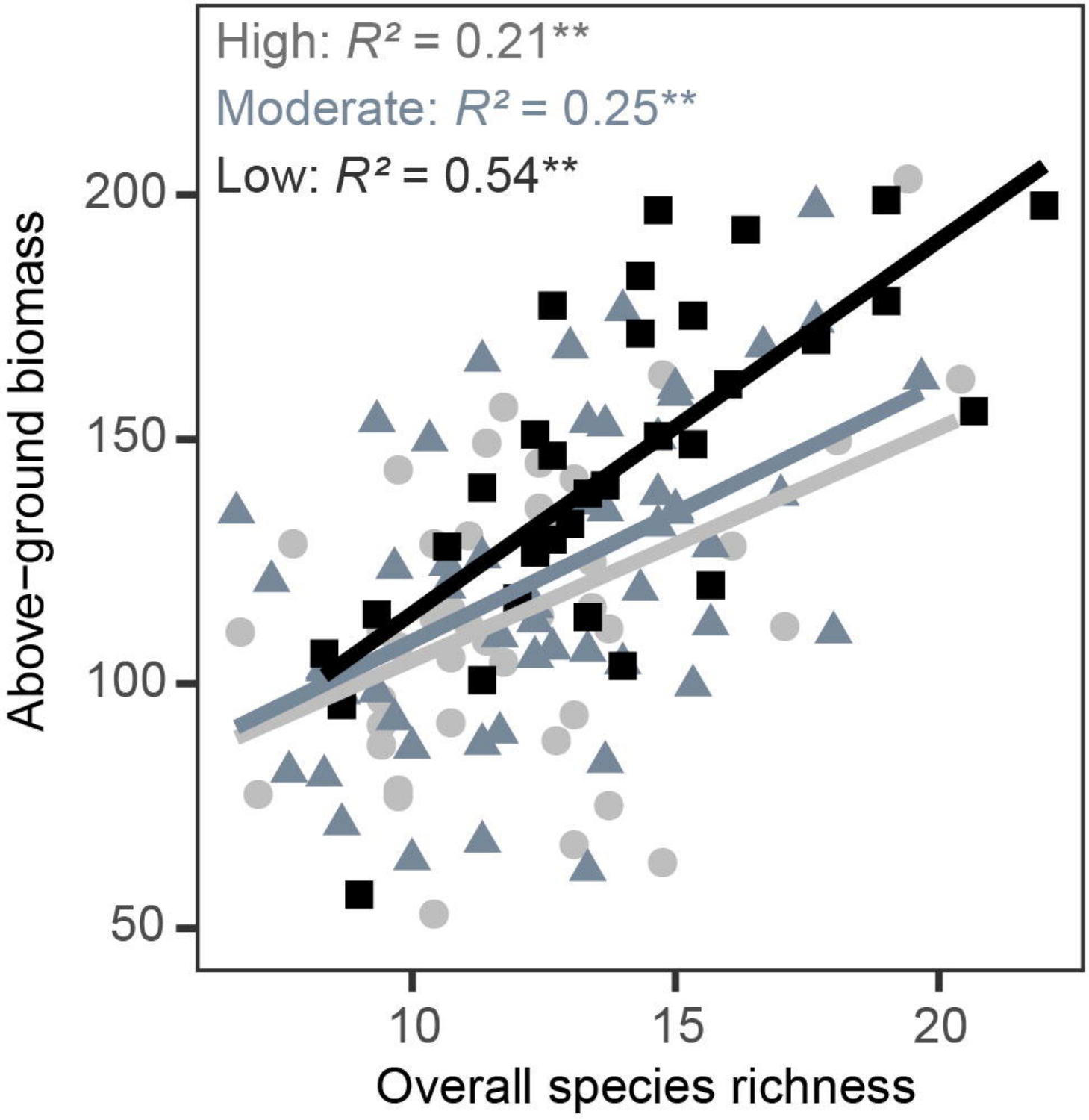

Habitat fragmentation
habitat loss and fragmentation per se
Percentage of specialists
Species richness
Above-ground biomass


Overall species
Grassland specialists
Weeds
(a)
R² = 0.05*, n = 130
R² = 0.17**, n = 130
R² = 0.10**, n = 130
Species richness
Habitat loss (%)
(b)
R² = 0.00, n = 130
R² = 0.03, n = 130
R² = 0.07**, n = 130
Species richness
Fragmentation per se (PC1)


Habitat loss
Fragmentation per se
Grassland specialist richness
Weed richness
*
**
**
−0.25
0.00
0.25
0.50
0.75
Standardized estimate



Fisher's C = 5.5, *P*-value = 0.48


High: R^2 = 0.21**
Moderate: R^2 = 0.25**
Low: R^2 = 0.54**
Above−ground biomass
200
150
100
50
10
15
20
Overall species richness