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RESEARCH ARTICLE

Island biogeography theory outweighs habitat amount hypothesis in predicting plant species richness in small grassland remnants

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Abstract

Context The habitat amount hypothesis has rarely been tested on plant communities. It remains unclear how habitat amount affect species richness in habitat fragments compared to island effects such as isolation and patch size.

Objectives How do patch size and spatial distribution compared to habitat amount predict plant species richness and grassland specialist plant species in small grassland remnants? How does sampling area affect the prediction of spatial variables on species richness?

Methods We recorded plant species density and richness on 131 midfield islets (small remnants of semi-natural grassland) situated in 27 landscapes in Sweden. Further, we tested how habitat amount, compared to focal patch size and distance to nearest neighbor predicted species density and richness of plants and of grassland specialists.

Results A total of 381 plant species were recorded (including 85 grassland specialist species). A combination of patch size and isolation was better in predicting both density and richness of species compared to habitat amount. Almost 45% of species richness and 23% of specialist species were explained by island biogeography parameters compared to 19 and 11% by the amount of habitat. A scaled sampling method increased the explanation level of island biogeography parameters and habitat amount.

Conclusions Habitat amount as a concept is not as good as island biogeography to predict species richness in small habitats. Priority in landscape planning should be on larger patches rather than several small, even if they are close together. We recommend a sampling area scaled to patch size in small habitats.

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Introduction

The importance of landscape structure on biodiversity and community composition has been highlighted within both theoretical and empirical ecological research (Lindenmayer and Fischer 2006; Mouquet et al. 2006; McGill 2010; Lindenmayer et al. 2015). This is of particular interest for conservation, as habitat loss and fragmentation are among the major current threats to biodiversity

worldwide (Foley et al. 2005; Ibanez et al. 2014). Land use intensification in agricultural landscapes has led to habitat destruction of semi- natural habitats. However, in many intensively used landscapes were much of the original habitats has disappeared we can still find small remnant habitats. Small, natural or semi-natural, remnant habitats in highly fragmented agricultural landscapes have been found to be important for both biodiversity and ecosystem services (Kleijn and Baldi 2005; Tscharntke et al. 2005; Cousins 2006; Mendenhall et al. 2014). They can function as both refugia and sources of dispersal for plants (Cousins and Eriksson 2001; Harrison et al. 2006; Dorrough et al. 2007; Prober and Smith 2009; Plue and Cousins 2013; Lindborg et al. 2014). In landscapes with little other remaining natural or semi-natural habitats, small remnant habitats appear to have an additive positive effect for biodiversity (Daily et al. 2003; Økland et al. 2006). As small remnant habitats contribute to diversity within fragments they may help to enhance biodiversity at the regional scale (Ricketts et al. 2001; Daily et al. 2003; Jakobsson et al. 2016) and thus mitigate negative effects caused by fragmentation and isolation in species-poor agricultural landscapes (Vandermeer and Perfecto 2007; Plue and Cousins 2013). In this context, small remnant habitats may fulfil important ecological functions for biodiversity, e.g. as stepping stones for dispersal (Honnay et al. 1998), and they might increase the general permeability in the landscape for certain species (Jakobsson et al. 2016).

In the contemporary intensively-used agricultural landscape, small remnant habitats can effectively be seen as islands and thus the concepts of the island biogeography theory (hereafter IBT) has been used to model the relationship between spatial pattern and species richness (Mayfield and Daily 2005; Santos et al. 2010; Laurance et al. 2012; Mendenhall et al. 2014; Burns 2015) and as a driver of genetic diversity in plants (McGlaughlin et al. 2014). The island biogeography theory stipulates that an island has an equilibrium numbers of species, and species richness increases with larger habitat area and with shorter distances to similar habitat types. An isolated, small habitat patch has a lower immigration rate and a higher extinction rate resulting in lower species richness compared to a larger or a less isolated habitat patch

(MacArthur and Wilson 1967; Mendenhall et al. 2014).

IBT was developed with oceanic islands in mind, and does not include heterogeneity of habitats on the islands or the composition of the surrounding landscape. Some of the shortcomings of IBT models have been overcome by incorporating landscape ecological principles (Laurance and Cochrane 2001; Ewers and Didham 2006; Ewers et al. 2010; Santos et al. 2010; Öckinger et al. 2012) such as matrix quality, and habitat spatial arrangement as these strongly influence both extinction and immigration processes (Åstrom and Pärt 2013; Rybicki and Hanski 2013). In this sense the spatial configuration of habitats can be even more important to population response than habitat area in highly fragmented landscapes.

Understanding how populations and communities respond to landscape structure is essential for maintaining biodiversity and managing ecosystems, particularly in highly fragmented landscapes, although many questions still remain on how communities respond to surrounding landscape structure and change. Fahrig (2013) suggested the "Habitat amount hypothesis" as a more straight forward view to model the relationship between habitat distribution and species richness in fragmented landscapes compared to habitat area and isolation (used in the island biogeography theory). The habitat amount hypothesis (hereafter HAH)) challenges the assumption that habitat patches are natural units to measure ecological responses to fragmentation and that species respond directly to habitat patch size and isolation (Fahrig 2013). Compared to the IBT, HAH lessens the importance of fragments spatial arrangement as a driver of species richness in a focal habitat. Further, the HAH (Fahrig 2013) stipulates that if the habitat is correctly defined in an appropriate extended landscape for the species, the HAH can replace measurements of area and configuration of habitats with one single measurement, the amount of habitat type in a specific landscape. According to HAH, species richness is correlated to focal patch area and the amount of the same habitat in the surrounding landscape Fahrig (2013) (Fig. 1), as this effects species colonization. Thus, fragmentation of the focal patch can be compensated by a larger amount of habitat within an appropriate distance. The appropriate distance is species specific.
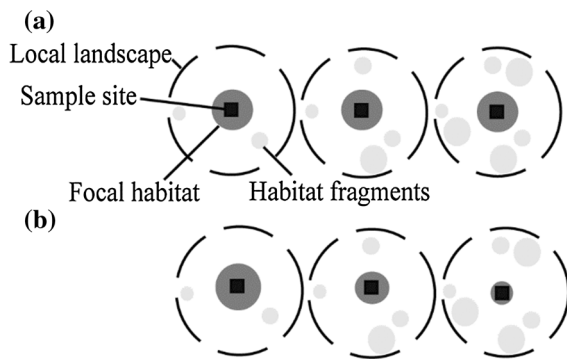
Fig. 1 According to *the habitat amount hypothesis* (Fahrig 2013) species density will **a** increase in a focal habitat patch if the amount of surrounding habitat increases, **b** stay the same if the focal patch area becomes smaller, but the area is compensated by a larger amount of surrounding habitat, i.e. if the total habitat amount remains the same in the local landscape. This is provided that the sampled area is constant in the focal patch, independent of the area of the focal patch

One important prerequisite in the HAH is that the sampling area is equal as the sampled species richness will increase with sampling intensity (Baasch et al. 2010; Azovsky 2011). It is argued that the same sampling effort in all patches will make it possible to separate the effect of focal patch size, isolation and surrounding habitat amount and sampling area effect on species richness in the focal patch (Fahrig 2013). This way of measuring species richness can be referred to as *species density* (Magurran and McGill 2011). Yet, by sampling a smaller part of the patch area there is an increasing risk of missing a larger amount of the total richness of the patch (de Solla et al. 2005), which may give advantage to a sampling effort that is scaled to the patch size.

However, the HAH has been challenged (Hanski 2015) as the significance of spatial configuration of fragmented habitat may vary with spatial scale. In Fahrig's paper, HAH was applied on multispecies community data including species with different habitat requirements which Hanski (2015) considered to be problematic. According to the metapopulation theory persistence and extinction dynamic of populations (single species) in fragmented landscapes are connected to the spatial connectivity of suitable habitats (Hanski 1999; Molofsky and Ferdy 2005). Both IBT and HAH primarily focus on the community level, whereas the commonly used metapopulation theory focus on single species populations dynamics between patches (Hanski 1999). Still, area of the patch and

distance between patches are important factors to model the dynamics. Area of the patch assumes to determine the extinction rate of the local population and isolation to determine the colonization rate. Though, models of single species is not enough if you want to understand how species richness of plants response to fragmentation and isolation of habitats.

Furthermore, theories and hypotheses on the effects of landscape structure and change have often been developed on much more mobile organisms compared to plants. Predicting plant dispersal within landscapes are difficult as their movement over long dispersal often occurs passively by water or wind, or are dependent on movement of other organisms (Auffret et al. 2017). To complicate matters further, remnant populations of specialist plant species and species composition in a habitat can be a reflection of former land use (Eriksson 1996; Helm et al. 2006).

So far, most studies on the effects of fragmentation have used variants of *Island biogeography theory* (MacArthur and Wilson 1967) and the *species-area relationship* where habitat area and distance to nearest similar habitat is measured. It is widely accepted that habitat area is important for biodiversity (Steffan-Dewenter and Tscharntke 2000; Drakare et al. 2006; Panitsa et al. 2006; Dengler 2009; Fattorini and Borges 2012). Still we know little on how much surrounding habitat amount influence species density (number of species per unit area) and richness (number of species on whole areas of habitat islands) in an area.

In this study, we used plant species density and richness on small remnants of semi-natural grassland habitats in agricultural landscapes to compare the habitat amount hypothesis with patch size and isolation (IBT). The small remnant habitats in the study are so-called midfield islets, which are small (up to 0.5 ha) bedrock or moraine outcrops surrounded by a matrix of crop-field. These habitats were in the past managed as a part of semi-natural grasslands, where hay was cut and livestock grazed after harvest. Today midfield islets are not managed but the encroachment of trees and shrubs is slow due to very dry soil conditions. Still, they may contain a surprisingly high amount of grassland plant specialists, both in the vegetation and in the seed-bank (Auffret and Cousins 2011; Plue and Cousins 2013). Therefore midfield islets have a great potential for future restoration of grassland communities but also they might also increase the species pool and the propagules of seeds in otherwise species-poor

agricultural landscapes. To our knowledge this is the first time midfield islets is used to identify patterns related to islands effects in comparison to the habitat amount effects on species density and richness of plants.

We asked, how does patch size and spatial distribution predict species density and richness of plants and also the density and number of grassland specialist species compared to surrounding habitat amount on small grassland remnants? How does sampling area affect the prediction of landscape variables on species richness?

Methods

The study region was situated in central Sweden, close to the capital Stockholm, (central point coordinates 59°35′09″N and 17°37′15″E). The region is characterised by a topography that ranges from the Baltic Sea level to higher land with maximum altitude of 150 m. The large lake Mälaren is located in the centre of the study region and has a moderating effect on local climate. The mean annual precipitation in the region is 500–600 mm, the mean temperature for January is −3 to −5 °C and for July 15–18 °C. Forest, arable land and lakes constitute the main part of the landscape today. Arable land is situated in the valleys which are filled with clay soils whereas the higher ground is dominated by coarser soils and forestry. The landscape has a long tradition of livestock grazing and haymaking. The area of semi-natural grassland used to be more extensive within the study region but has decreased by >90% during the last 100 years (Cousins et al. 2015). Despite being one of the most urbanized areas in Sweden, 42% of the study area is forest, 22% crop field and 4% grazed semi-natural grassland.

Landscape data

Twenty-seven agricultural study areas (circles with radii of 500 m) between 1.9 and 9.7 km apart were selected under the condition that at least one midfield islet were situated in the field. All midfield islets within these study areas were identified using recent infra-red aerial photos (2010–2013) and digitalized in Stereo Analyst for ArcGIS (ESRI, Redlands CA, USA). In total of 297 midfield islets with areas of 17–4876 m^2 (median = 427 m^2) were identified.

From the 297 midfield islets we selected 131 focal midfield islets with an area of >150 m^2 (area 163–4876 m^2, median = 1146), resulting in the same number of local landscapes (Fig. 2), situated in twenty-seven study areas. Smaller islets, than 150 m^2, consist to a large part of stones or bedrock with little or no vegetation and were considered to be too small to be included in the survey. Degree of isolation of each midfield islet was measured as the distance to the nearest midfield islet (1–568 m, median 33 m).

Plant sampling

All plant species in the field layer of the 131 midfield islets were recorded from mid-June to end of July 2013.

Species density

One important prerequisite using *the habitat amount hypothesis* is that the sampling effort is uniform (Fahrig 2013), thus the 131 focal midfield islets were all sampled using eight plots of 0.5 × 0.5 m (Fig. 2), hereafter called *uniform sampling*. When arriving to a midfield islet the first plot was randomly distributed. All plants, in the plot in the field layer were noted. Presence-absence data on all vascular plants (height <50 cm) in the plots were noted, often referred to as the *species density* in an equally sampled area on all the midfield islets. To capture as many plant taxa as possible in each habitat the next plot was placed 3 m away, and were preferably placed were there was at least one additive species to the species list. Nomenclature follows Krok and Almquist (2013). Afterwards grassland specialists' species were categorised according to Ekstam and Forshed (1992). Species in the successional categories (for dry and moist habitats) were A- species which already in an early phase decreases in quantity and B-species which during an intermediate phase in the succession decrease in quantity, are hereafter called grassland specialist species.

Species richness

Between 8 and 25 plots were distributed, proportional to midfield islets patch size. The species from the scaled sampling effort was supplemented with species
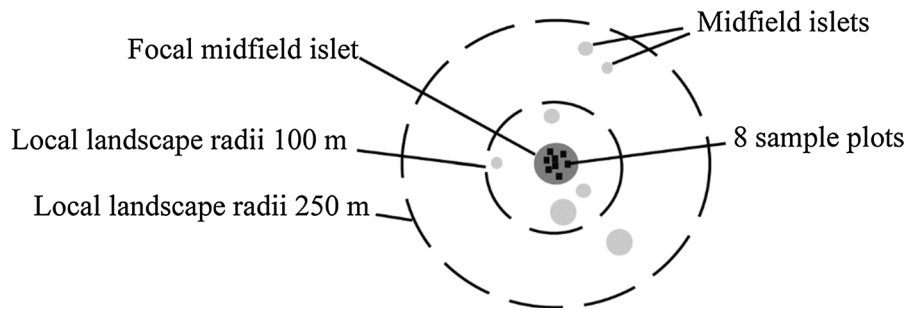
Fig. 2 Sampling design of the study. On each focal midfield islet all plants in the field layer in 8 plots 0.5 × 0.5 m were recorded. Additionally, the total species richness (α richness) of the focal midfield islet was sampled. Area of the focal patch and distance to the nearest neighbor were measured, as well as the habitat amount of midfield islets in two distances (100 and 250 m) from the midpoint of the focal midfield islet

identified on the midfield islets by walking slowly, carefully observing all species not recorded in the plots, giving the *species richness* of the whole midfield islet, hereafter called *α richness*.

Landscape variables

To test the response variables, species density, α richness, density and number of specialist species, three explanatory variables were calculated for each focal midfield islet: (1) area of the focal midfield islet (n = 131), (2) distance to the nearest other midfield islet, (3) the total area of midfield islets in a circle (from a centre point on the focal midfield islet). To identify at what distance the surrounding habitat amount had the strongest effect on species density, α richness, density and number of specialist species, two circles of different sizes were used. The radii of the circle were chosen to be 100 and 250 m from the midpoint of the midfield islet, as plants have a relatively short dispersal distance (Tackenberg 2003; Krauss et al. 2004; Schleicher et al. 2011). A smaller circle would not include any other area than the focal midfield islet (radius of the largest islet = 65 m). Size of the midfield islets and the amount of midfield islets within two circles, of 100 and 250 m radii from a centre point on the focal midfield islets (Fig. 2), were calculated in ArcGIS 10.2 (ESRI, Redlands CA, USA).

Data analysis

A correlation test was performed (Spearmańs rank correlation coefficient tests) to measure the correlation between species density, α richness, density and number of specialist species, and predictor variables (area, distance to nearest midfield islet and habitat amount in a circle of radii 100 and 250 m), one by one (Table 1) and between the predictors to identify collinearity. The procedure was used for species density based on the uniform sampling and species richness (α richness) based on the scaled sampling (Spearman's rank correlation coefficient test, Table 1). Area of focal midfield islet was slightly correlated with distance to the nearest midfield islet (−0.192, p = 0.03). As the standard errors of the coefficients of the model did not change when using both area and distance in the model, compared to just one of them, the variables were considered acceptable to use both in the same model (Appendix S1). As the habitat amount within the smaller circle (radii 100 m) had a higher correlation to all response variables (species density, α richness, density and number of specialist species) compared to the 250 m radius, the smaller circle was used in further modeling (Table 1).

Effects of the explanatory variables (area, distance to the nearest midfield islet and habitat amount) on the response variables, (species density, α richness, density and number of specialist species, number of midfield islets = 131) were tested using generalized linear models (GLM) with stepwise selection of the best fitted model. The error distribution model was defined as Poisson with correction of the standard errors using quasi-GLM model where the variance is given by ø * μ, and were μ is the mean and ø is the dispersion parameter, as over-dispersion was detected (Zuur et al. 2009). The stepwise selection was based

Table 1 Spearman's correlations between plant species density and species richness, specialist species and patch size, isolation and habitat amount within two distances (100 and 250 m) from a midpoint of the focal habitat

	Patch size		Isolation		Habitat amount (100 m)		Habitat amount (250 m)	
	ρ	p value	ρ	p value	ρ	p value	ρ	p value
Uniform sampling effort								
Species density	0.30	**<0.001**	−0.25	**0.004**	0.27	**0.002**	0.20	**0.023**
Density of specialist species	0.29	**<0.001**	−0.26	**0.003**	0.31	**<0.001**	0.20	**0.020**
Patch size	–	–	−0.19	**0.03**	0.65	**<0.001**	0.34	**<0.001**
Scaled sampling effort								
α richness	0.70	**<0.001**	−0.18	**0.04**	0.50	**<0.001**	0.29	**<0.001**
Number of specialist species	0.51	**<0.001**	−0.18	0.05	0.39	**<0.001**	0.20	0.18

In the uniform sampling effort, species in 8 plots (0.5 × 0.5 m) are included (species density). In the scaled sampling effort, all plants on the midfield islet are included (α richness). Bold letters indicate significance with $p < 0.05$

on p values. A subsequent Chi square test was performed to identify the best fitted model to explain species diversity, α richness and diversity and number of specialist species on the midfield islets by comparing the percentage of explained deviance. The power of the two final models, one expressing the IBT and the other the HAH, were compared by *percentage of explained deviance*. The higher the value the better the fit. The percentage of explained deviance was calculated as follows: (null deviance-residual deviance) × 100/null deviance. Where the null deviance explains how well the model predicts the response with only the intercept. The residual deviance explains how well the model predicts the response when all predictors are included (Favre-Bac et al. 2014).

Statistical analyses were carried out using R 2.14.1 (R Development Core Team 2011; package vegan, function: *vegdist* and package lme4, functions: *lm* and *glm*).

Results

Based on the uniform sampling (eight plots of 0.5 × 0.5 m) of 131 focal midfield islets we recorded 299 plant species in total. Among these, 74 were classified as grassland specialist species. Mean ± SD species diversity (in eight sample plots) was 32 ± 8.0 and 7 ± 4.1 grassland specialist species. Species density varied between 1 and 19 species (mean 8.0 ± 2.8 SD) in each sampled plot (0.25 m²). When

sampling total midfield islet richness in the study we found 381 plant species (gamma richness) of which 85 were grassland specialists. α richness varied between 30 and 84 species (mean 49.7, ± 16.1 SD) including 0–32 grassland specialist species (mean 11.6, ± 6.2 SD) per midfield islet (area 163–4876 m²).

We analyzed species data, based on the uniform sampling effort, and the relationship to the different landscape variables. We found a relationship between species density and density of specialist species to the surrounding habitat amount. Comparing the two distances, within the habitat amount were calculated, the smaller circle with a radii of 100 m had the strongest relationship with species density and density of specialist species (species density $p < 0.004$, density of specialist species $p < 0.003$, Appendix S1) compare to the larger circle of 250 m (species density $p < 0.016$, density of specialist species *non-significant*, Appendix S1). The distance of 100 m was therefor considered to be the distance at which the amount of habitat had the largest effect. When we analyzed the species density according to patch size and isolation, we found that patch size had the same effect size ($p = 0.002$) as isolation on species density (Appendix S1). On species density of grassland specialist species the effect of the patch size ($p = 0.004$) was slightly larger than the effect of isolation ($p = 0.009$, Appendix S1). Increasing distance to the nearest midfield islet influenced species density negatively.

When comparing the models the explanation level of species density and density of specialist species was

low. The percentages of explained deviance by the best fitted models for total species density and density of grassland specialist species were highest for the model including the area of the focal midfield islet together with distance to the nearest other midfield islet (total richness 12.5%, *p = 0.005,* specialist species 9.9%, *p = 0.016*, Table 2). Habitat area (7.0%, *p = 0.002*) alone, or the distance to the nearest midfield islet (7.7%, *p = 0.001*) affected species density more than surrounding habitat amount (6.1%, *p = 0.004,* Table 2). The number of specialist species was less well predicted by area (5.9%, *p = 0.004*) or distance (5.7%, *p = 0.005*) compared to surrounding habitat amount (6.2%, *p = 0.003*) in a circle with a radii of 100 m (Table 2).

Similar to species density, the smaller circle, in total, had the strongest relationship to species richness and number of grassland specialist species (species richness *p < 0.001*, number of specialist species *<0.001*) compared to the larger circle of 250 m (species richness *p < 0.001*, number of specialist species: non-significant). When using the species list of the whole midfield islet the explanation level increased compared to the uniform sampling effort (Table 2, 3).

Habitat area explained 41.1% (*p < 0.001*) of the deviance in species richness and 20.6% in the total number of specialist species (*p < 0.001*) (Table 3). Habitat amount within a radius of 100 m explained 18.9% of species richness (*p < 0.001*) and 11.1% of richness of specialist species (*p < 0.001*). Habitat area

together with distance to nearest midfield islet increased the percentages of explained deviance for the best fitted models to 44.8% for species richness (*p = 0.004*) and 23.1% for richness of specialist species (*p = 0.041*) (Table 3). The increase of the relationship between area and species richness when scaling the sampling area to the patch size was higher in richness of plants then in richness of just specialist species (Fig. 3).

Discussion

In this study we found 381 plant species, of which 22% were grassland specialists, within a total area of 20 ha distributed on 131 small, relatively isolated remnant habitats that have not been managed as grasslands for several decades. *The habitat amount hypothesis* (Fahrig 2013), challenges the assumption that habitat patches are natural units to measure ecological response to fragmentation and the assumption that species respond directly to patch size and isolation (the *island biogeography theory*). However, based on plant species density and richness in small remnant habitats in fragmented agricultural landscapes, our study suggest that island biogeography theory, i.e. size and isolation, more accurately explain the patterns of species density and richness as well as density and richness of specialist species. Increasing patch size and decreased isolation had a larger effect on species density and richness of plants compared to a larger

Table 2 Comparison of models of the relationship between spatial and local factors on plant species density (uniform sampling effort) in the field layer and species richness of grassland specialist species on midfield islets based on a Chi square test

Model	Species density				Density of specialist species			
	Df	Residual deviance	*p* value	ED (%)	Df	Residual deviance	*p* value	ED (%)
Intercept	130	265.4	**<0.001**		130	317.6	**<0.001**	
Patch size	129	246.9	**0.002**	**7.0**	129	299.0	**0.004**	**5.9**
Isolation	129	244.9	**0.001**	**7.7**	129	299.5	**0.005**	**5.7**
Habitat amount 100 m	129	249.2	**0.004**	**6.1**	129	297.8	**0.003**	**6.2**
Patch size + isolation	128	232.3	**0.005**	**12.5**	128	286.2	**0.016**	**9.9**
Patch size + isolation + (patch size × isolation)	127	n.s.	n.s.		127	n.s.	n.s.	

Percentage of explained deviance (ED %) were calculated as follow: (null deviance-residual deviance) × 100/null deviance. Bold letters indicate significance with *p < 0.05*

n.s. Non-significant

Table 3 Comparison of models of the relationship between spatial and local factors on plant species richness (α richness of the whole midfield islet) and species richness of grassland specialist species on midfield islets based on a Chi square test

Model	Species richness				Specialist species			
	Df	Residual deviance	p value	ED (%)	Df	Residual deviance	p value	ED (%)
Intercept	130	682.6	**<0.001**		130	440.5	**<0.001**	
Patch size	129	402.1	**<0.001**	**41.1**	129	349.7	**<0.001**	**20.6**
Isolation	129	621.7	**<0.001**	**8.9**	129	416.8	**0.007**	**5.4**
Habitat amount 100 m	129	553.8	**<0.001**	**18.9**	129	391.6	**<0.001**	**11.1**
Patch size + isolation	128	376.8	**0.004**	**44.8**	128	338.5	**0.041**	**23.1**
Patch size + isolation + (patch size × isolation)	127	n.s.	n.s.		127	n.s.	n.s.	

Percentage of explained deviance (ED %) were calculated as follows: (null deviance-residual deviance) × 100/null deviance. Bold letters indicate significance with $p < 0.05$

n.s. Non-significant

Fig. 3 Increase of species density and α richness of all plants in the field layer and of specialist species in relation to increased area when the sampling effort is scaled after habitat size (α richness $R^2 = 0.46$, $p < 0.001$, richness of specialists $R = 0.23$, $p < 0.001$) and when sampling an uniform area (eight 0.5 × 0.5 m), regardless of habitat size (species density $R^2 = 0.07$, $p = 0.002$, density of specialists $R = 0.07$, $p = 0.002$)
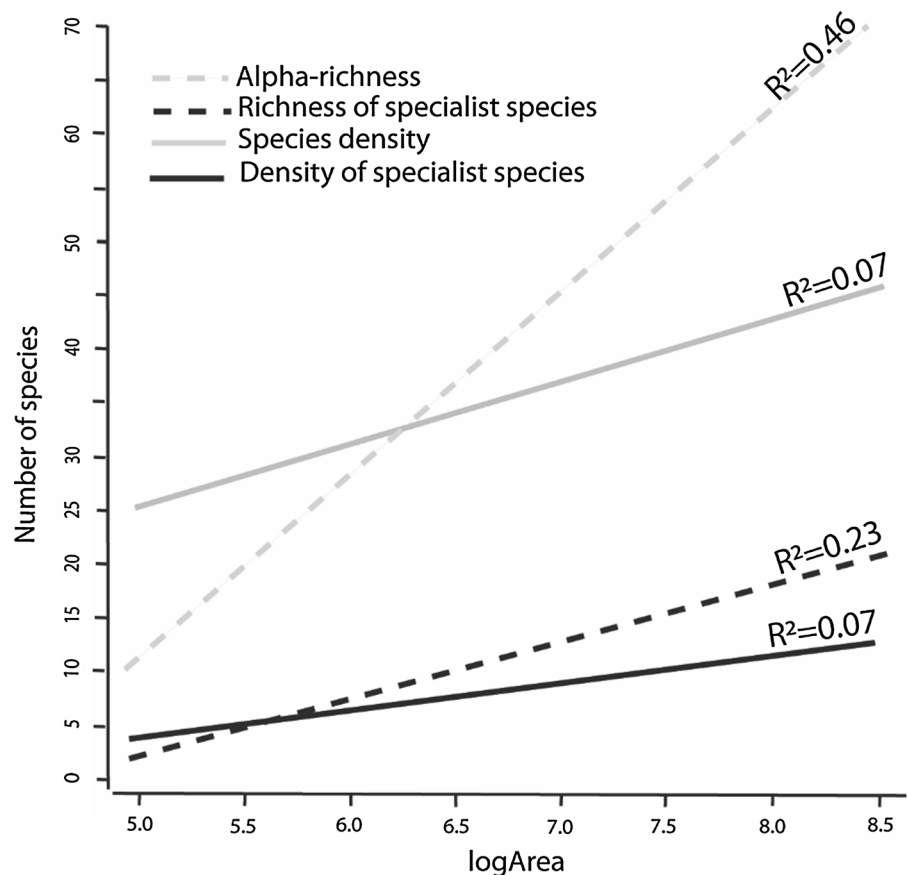
amount of habitat in the near surroundings (within 100 m). Our results show that configuration of habitats cannot be ignore when predicting species richness in

fragmented habitats. Evju and Svedrup-Thygeson (2016) investigated the effects of habitat size, distance to similar habitats, and surrounding habitat amount on

grassland plant specialist richness in grasslands in Norway. Although they investigated larger managed grasslands with wider buffer-zones of habitat amount (500–3000 m in the surrounding) than those in our study, they still found similar effects. Patch size and distance to the nearest similar patch were more important to grassland specialist richness than surrounding habitat amount (Evju and Sverdrup-Thygeson 2016). Thus our results may also apply to larger scales, despite the fact that plant species have been shown to respond more strongly to local surroundings (Krauss et al. 2004) and rarely disperse over longer distances (Tackenberg 2003).

Despite that both size, isolation and surrounding habitat amount influence plant species density on small remnant habitats, the coefficient of determination was low unless α richness of the whole midfield islet was used. Thus, the amount of unexplained factors that influence α richness on midfield islets is high, as it often is when analysing the effect of spatial factors (Gazol and Ibanez 2010; Zelnik and Carni 2013; Sitzia et al. 2014). For example, Sitzia et al. (2014) found that 0–9% of the variation in α richness in woody field margins is due to spatial variables such as the proportion of surrounding agricultural land use. When analyzing α richness, increased patch size increased explanation percentage which can be due to a sampling effort effect (Fig. 3) which can be argued as an overestimation of habitat quality. Yet, midfield islets differ largely in size (area 163–4876 m^2). A larger area include a larger variation of microhabitat, which leads to more niches and higher species richness. Additionally, many species have a clustered distribution of species that will affect the possibility for species to be detected in a limited number of small sampling plots (Plue et al. 2012). The variation between midfield islets would not be apparent if the sampling area covers a too small part of the patch. However, by increasing the sampling area more generalist species are included whereas a relatively small proportion of grassland specialists were detected.

In this study, the size together with isolation of midfield islets had a larger effect on plant species density and richness compared to the density or richness of specialist species. Generalist species often have broader niche requirement than specialist species and it is possible that immigrating generalist species from the surroundings landscape cause the difference in effect size. Specialists have been found to be more

related to habitat and landscape spatial structure compared to generalists plant species (Harrison et al. 2006; Miller et al. 2015). The percentage of explained deviance increased if the sampling effort is scaled to the area, both for α richness and richness of grassland specialist species compared to species density of plants in general or that of specialists. Specialist plant species are adapted to a specific habitat or management (Ekstam and Forshed 1992), which in our case of grassland specialist species is grazing or mowing. There are few semi-natural grassland or remnant grassland habitats left in these landscapes and grassland specialists are often poor long distance dispersers (Ozinga et al. 2009; Jamil et al. 2013; Lindborg et al. 2014; Purschke et al. 2014). Time since fragmentation and land use change may affect species richness and particularly, grassland specialist species on midfield islets. A larger patch would theoretically increase the probability for lasting, viable species populations. Core areas in large patches can usually hold more species that are more dependent of a continuous habitat type or land use (Tjørve 2010). Rare, specialized plant species are therefor usually found in large patches (Fukamachi et al. 1996; Tjørve 2010; Roesch et al. 2015). On the other hand, as patch size have been shown to affect the speed of extinction, smaller fragments can be more sensitive as turnover is quicker (Fahrig 2001; Kuussaari et al. 2009; Hylander and Ehrlén 2013; Bommarco et al. 2014). In this study, the largest fragment was 4876 m^2. We found that surrounding habitat amount had almost the same effect as size (alone) on grassland specialist species compared to focal patch size (patch size together with isolation still have the strongest relationship to both density and richness of specialist species). One reason could be that larger midfield islets often have more trees and therefore poorer light conditions which negatively affects plant species richness (Harrison et al. 2006) and particularly many grassland specialist species. Smaller islets usually have a thin soil layer and more recurring drought which results in slower encroachment of more competitive plants and are therefore more suitable habitat for light demanding grassland specialist species (Cousins 2006). As generalist species have broader spectra of demands of light availability, they can use more of the area of the midfield islet, and not just the open areas.

In conservation planning it is necessary to direct efforts to where the outcome is the most profitable.

The habitat amount hypothesis have been suggested to be a simple and quick way to predict species richness in fragmented habitats. However our study suggest that patch is a better predictor of species richness than habitat amount in the surrounding landscape, except for species density of grassland specialist species.

Conclusions

The habitat amount is not as effective as patch area combined with distance to the nearest other patch to predict species richness of plants or grassland specialist species. Patch isolation influence on species richness and therefor the configuration of habitats should be taken into account when analyzing plant species richness in fragmented habitats. If a more straightforward measurement is wanted, patch size alone is a simple and good predictor for plant species richness and richness of specialist species. Further, we recommend a sampling area scaled to patch size in small habitats, for an optimal estimation of species richness.

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