

# Plant species occurrence in a fragmented grassland landscape: the importance of species traits

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**Abstract** Anthropogenic habitat modification and fragmentation is considered one of the most serious threats to biodiversity. To develop effective conservation strategies towards such pressures we need to improve our understanding of how species richness and community composition are shaped by species' responses to landscape patterns. In this study we tested relationships between patch size and isolation, species richness and species traits in a fragmented landscape of calcareous grasslands—a diversity hotspot in Southern Norway. We recorded a total of 381 vascular plant species, of which 50 are considered habitat specialists, distributed among 86 habitat patches (50–9,475 m<sup>2</sup>) in 22 of 50 randomly sampled 500 × 500 m-plots. We found that large habitat patches held more species of both generalists and specialists than small habitat patches and that well-connected patches held more specialist species than isolated patches. About 1/3 of the habitat specialists in this study system showed vulnerability to isolation, i.e. lower probability of occurrence in isolated patches. Traits related both to persistence (short lifespan) and colonization ability (low seed production per plant) were predictors of vulnerability to isolation. Our results indicate that both colonization and extinction processes affect species composition and richness, and that the rescue-effect—mitigation of local, area-dependent extinctions through colonization—is reduced in isolated patches. These findings suggest that conservation strategies should place greater emphasis on the spatial configuration of the habitat network, and on the preservation of colonization processes to ensure regional persistence of species.

**Keywords** Connectivity conservation · Fragmentation · Functional traits · Life-history · Plant diversity · Species-area effect

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## Introduction

Anthropogenic habitat modification represents the most important cause of habitat loss and fragmentation (Fahrig 2003), and such landscape changes represent one of the most serious threats to biodiversity (Foley et al. 2005; Rockstrom et al. 2009). Habitat protection is an established conservation measure that can alleviate the negative effects of land use changes. Lately, the spatial patterns and functional connectivity within a network of protected areas have received increased attention, both in ecology and in international policy initiatives. The international Aichi Biodiversity Targets state that the areas of particular importance for biodiversity and ecosystem services are to be conserved through “ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures” (Convention on Biological Diversity Strategic plan for biodiversity 2011). To fulfill this target we need to improve our understanding of how species and communities respond to spatial patterns in the landscape, based on empirical research.

Island biogeography and metapopulation dynamics predict that species persistence in fragmented habitats depend on local colonization and extinction processes (MacArthur and Wilson 1967; Levins 1969). As habitat loss leads to decrease in size of fragments and increased fragment isolation, it reduces local population sizes and rates of colonization and enhances the risk of local extinctions (Hanski 1998; Fahrig 2003; Rybicki and Hanski 2013). Consequently local species richness can be expected to decrease as habitat patch size is reduced and distance between habitat patches is increased (MacArthur and Wilson 1967; Losos and Ricklefs 2009). A more relevant question for conservation management than species richness per se is species composition, i.e. which species are likely to persist or disappear when habitats are lost (Hobbs and Yates 2003). Classical metapopulation models (Levins 1969; Hanski 1994) take the perspective of individual species but do not consider in detail how species differ beyond local persistence and colonization abilities. Recent literature reviews emphasize that species respond differently to habitat loss and fragmentation depending on their life history strategies (Hobbs and Yates 2003; Henle et al. 2004; Ewers and Didham 2006), and several characteristics are predicted to predispose species to vulnerability to fragmentation (Table 1).

Firstly, plant species with a high habitat specificity—habitat specialists—will experience their habitat as more fragmented compared to generalist species, which have a higher probability of occurring also in the surrounding landscape (Henle et al. 2004; Ewers and Didham 2006). Consequently, species with narrow habitat requirements are predicted to be more strongly affected by habitat fragmentation than generalist species (Andrén et al. 1997). Furthermore Adriaens et al. (2006) found the species richness of habitat specialists, but not of generalists, to be negatively affected by isolation in fragmented calcareous grasslands in Belgium. Secondly, the capacity of plants to colonize suitable habitat patches depends on their reproductive potential (Turnbull et al. 2000) and their dispersal range (Johst et al. 2002; Nathan 2006). With a low number of offspring, colonization rates are reduced, making species with a low reproductive potential more prone to negative effects of habitat fragmentation (Higgins et al. 2003; Henle et al. 2004). Low reproductive potential is also frequently associated with low population growth, which reduces the probability of successful establishment of a population (Henle et al. 2004). A high dispersal capacity increases the probability of recolonizing habitat patches in the landscape and may increase the long-term persistence of species in a fragmented landscape (Johst et al. 2002; Verheyen et al. 2003). Finally, traits that positively affect plant population persistence, such as long lifespan, iteroparity (the ability to flower more than once), clonal

**Table 1** Overview of the traits used in the analyses. The traits are hypothesized to predispose species for vulnerability to fragmentation

Trait	Predisposing for sensitivity to fragmentation	Analog trait	Description	Scale	% of species	Source
<b>Habitat requirements</b>						
Habitat requirements	Narrow habitat requirements	Habitat specialist	Species confined to dry calcareous in the study area (1), generalist species (0)	Binomial	100	Lid and Lid (2005), expert judgment
<b>Reproduction</b>						
Reproductive potential	Low reproductive potential	Seed number	No. of seeds per rame/plant	Continuous (log <sub>2</sub> -transformed)	85	Kleyer et al. (2008)
<b>Dispersal</b>						
Dispersal capacity	Low dispersal capacity	Dispersal agent	1. Wind-dispersed, 2. non-wind dispersed	Nominal	91	Lid and Lid (2005), Fitter and Peat (1994)
Dispersal capacity	Low dispersal capacity	Seed mass	Weight of germinule (mg)	Continuous (log <sub>2</sub> -transformed)	94	Kleyer et al. (2008)
<b>Persistence</b>						
Lifespan	Short lifespan	Lifespan	1. Annual or biennial 2. Perennial	Nominal	100	Lid and Lid (2005)
Clonal reproduction	No clonal reproduction	Clonality	1. Little or no vegetative spread 2. Shortly creeping 3. Far creeping	Ordinal	91	Lid and Lid (2005), Fitter and Peat (1994)
Seed bank	No/short-lived seed bank	Seed bank longevity	Fraction of seed bank studies finding a persistent seed bank	Continuous	97	Seed bank longevity index (Bekker et al. 1998) calculated based on seed bank study data from Kleyer et al. (2008)

Habitat requirement is scored for all species in the dataset, but the remaining traits are scored for the habitat specialists only.

The table shows which easily measured traits are used as analogs to the traits, a description of the traits, their scale and the percentage of habitat specialists in our sample with values for the traits, as well as the data source of information

reproduction and long-lived seed banks, may allow the formation of remnant populations that persist over long periods of unfavourable environmental conditions and low recruitment rates (Eriksson 1996; Lindborg et al. 2005). Traits enhancing population persistence may thus decrease the species' vulnerability to fragmentation on a short-term scale. If environmental perturbations result in permanently unfavourable conditions, this can lead to delayed extinctions, also called extinction debt (Fahrig 2002; Kuussaari et al. 2009; Cousins and Vanhoenacker 2011; Hylander and Ehrlén 2013). Short-lived species respond more rapidly to changes in environmental conditions than long-lived (Morris et al. 2008) and have higher extinction rates (Ehrlén and van Groenendael 1998).

In this study, we use dry calcareous grasslands to study the importance of plant traits for vulnerability to fragmentation among vascular plants with high habitat specificity (habitat specialists). Calcareous grasslands are among the most species-rich habitats in northern and central Europe. Several calcareous grassland types are listed as priority habitats for conservation under the EU Habitats Directive (Wolking and Plank 1981; LIFE 2008). They face severe threats both from habitat loss and habitat degradation (e.g. shrub invasion, afforestation, and agricultural intensification). In order to safeguard the calcareous grasslands we need a better understanding of the interplay between patch size and patch isolation on species richness and composition in these habitats.

We use a study system of dry calcareous grasslands in the Oslo area, Southern Norway, where land use pressure has been, and still is, substantial. The distribution of dry calcareous grassland in the study area is naturally fragmented with several of the habitat patches located on islands in the Oslo fjord. Anthropogenic impact, through habitat conversion and degradation, has resulted in a further reduction in the mean habitat patch size and an increase in the mean patch isolation. A critical threshold of fragmentation can be reached where the distribution of habitat patches no longer coincides with the migration patterns of the species and metapopulation dynamics are disrupted (Hanski et al. 1995; With and Crist 1995). At this threshold level the probability of population extinction increases sharply (Fahrig 2001; Swift and Hannon 2010). However, no common threshold value exists across species and habitats (Fahrig 2001). Our aim is to investigate how the current spatial pattern of dry calcareous grasslands within this area affects the species richness of plants. Using information on species characteristics, we investigate the relationship between plant traits and response to spatial patterns. Specifically, we address the following questions: (1) How does the richness of generalist and specialist plant species respond to size and isolation of remaining patches of dry calcareous grasslands? (2) Can the response of individual habitat specialist species to habitat fragmentation be explained by species characteristics such as longevity and reproductive capacity, and if so, does it match the theoretical predictions of traits predisposing for vulnerability to fragmentation? And finally (3) How can our results improve management decisions on which patches to prioritize for conservation, in an area under a major land use pressure?

## Materials and methods

### Study area

The study was carried out in the inner Oslo fjord, in the counties of Oslo and Akershus, Norway (Fig. 1). The habitat dry calcareous grasslands in Norway is restricted to bedrock sites dating to the period from Cambrian to Silurian, and mainly found in a narrow zone between the sea and the forested inland areas. The habitat is frequently exposed to drought

due to a combination of high soil drainage and exposure to wind and sun. This, combined with effects of land rise and former grazing, creates the characteristic vegetation type. Dry calcareous grasslands in the inner Oslo fjord have a high occurrence of nationally red-listed species, including vascular plants, lichens, fungi and invertebrates.

Due to the dependency on bedrock qualities, exposure and a warm and dry climate, dry calcareous grasslands are naturally fragmented in the study area, and many of the habitat patches occur on islands in the Oslo fjord (Fig. 1). The Oslo fjord area is also the most densely populated area of Norway. Human impact, primarily through housing and infrastructure, has led to habitat loss with a reduction in habitat patch sizes and increased distances between them. Other important threats to the dry calcareous grasslands in the study area include recreational use (trampling, soil erosion), invasive species, and natural succession (transition to forest) as a result of the cessation of livestock grazing in the Oslo fjord area.

### Habitat patch data

The mapping of dry calcareous grasslands in the study area is ongoing. Therefore, information on the occurrence of dry calcareous grasslands is not spatially comprehensive yet. We mapped a sample of dry calcareous grassland habitat patches by superimposing a grid system of  $500 \times 500$  m plots on the study area giving a total of 238 plots (islands less than  $0.25 \text{ km}^2$  were treated as one sampling unit even if they were intersected by the sampling grid). The plots were numbered from 1–238, and using a random number generator we selected 50 plots for field inventory. In 22 of the plots we found dry calcareous grassland, and a total of 93 habitat patches were surveyed and digitized.

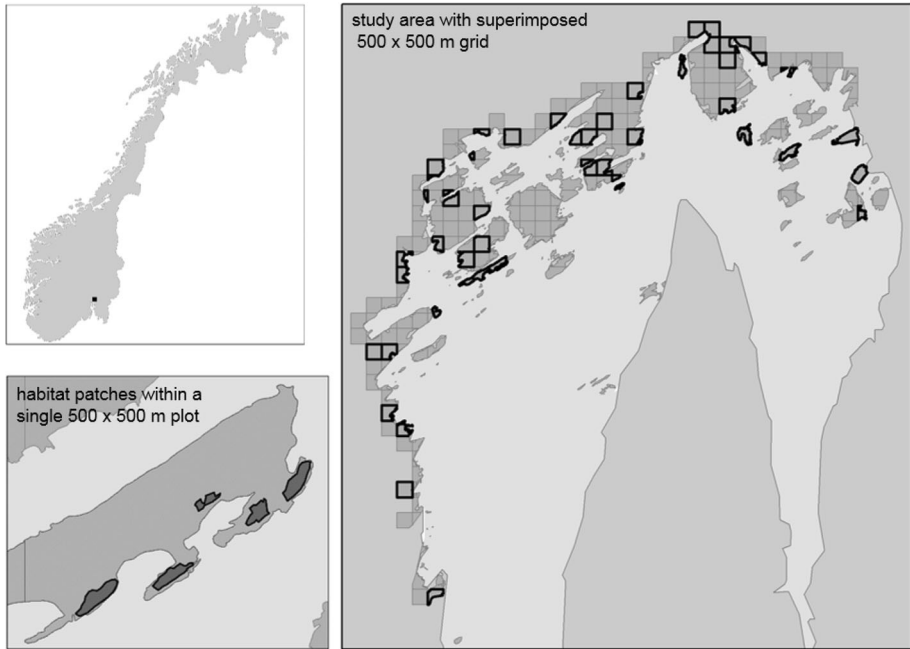
In order to fill the gaps for the analysis of connectivity, we merged data mapped in the field with a predictive habitat distribution model developed by Wollan et al. (2011). After a validation of the model based on presence/absence information from the mapped  $500 \times 500$  m plots, areas with a prediction value above 0.62 outside the mapped  $500 \times 500$  m plots were classified as dry calcareous grassland habitat. Above the chosen value, the area of correctly predicted presences increased significantly, while the amount of (wrongly predicted) absence decreased respectively. However, through the validation we also found an overestimation of occurrence of dry calcareous grasslands in the areas delineated from the model of about four times the mapped area of occurrence. Therefore, we downscaled the area of habitat polygons delineated from the prediction model by a factor of 0.25.

### Connectivity

We calculated the connectivity  $S_i$  of the 93 surveyed habitat patches to all patches  $j$  within a radius of 1 km of the patch centroid as:

$$S_i = \sum_{j \neq i} \exp(-\alpha \cdot d_{ij}) \cdot A_j$$

where  $A_j$  is the area of patch  $j$  (ha),  $d_{ij}$  is the distance between the centroids of patches  $i$  and  $j$  (km), and  $\alpha$  is the parameter of the exponential distribution setting the influence of distance on connectivity. Since we calculate the connectivity for a set of species differing in dispersal capacity, we set  $\alpha = 1$  (cf. Hanski 1994), which also makes our results comparable to previous studies in grasslands (e.g. Cousins et al. 2007; Lindborg 2007). The



**Fig. 1** Study area location in Norway (upper left), an overview of the study area with the superimposed grid, with randomly selected 500 × 500 m plots marked in bold (right) and a zoom-in on one 500 × 500 plot with delineated habitat patches (lower left)

1 km radius was chosen as it is commonly used in grassland studies (e.g. Cousins et al. 2007; Lindborg 2007), and represents the area that may affect species richness at the patch scale. However, the rank order of patch connectivity was similar if all patches within the study area were included, as opposed to including only patches within the 1 km-radius.

#### Vascular plant species data

In each habitat patch we recorded the occurrence of all vascular plants present. Seven of the habitat patches were incompletely surveyed and were excluded from further analyses. Fieldwork was carried out in June–July 2009 and 2010.

We defined the species to be either habitat specialists, that is, species which are strongly confined to the habitat dry calcareous grasslands within the study area, or generalists (occurring in a range of habitats) based on information in the flora (Lid and Lid 2005) and own knowledge of the species (Table 2). To characterize the habitat specialist species we selected six plant traits important for plant reproduction, dispersal and persistence (cf. Weiher et al. 1999), which represent analogs to the characteristics hypothesized to be important predictors of vulnerability to fragmentation (Henle et al. 2004; Table 1). Reproductive potential was represented by seed number, defined as the number of seeds per ramet/plant. Dispersal capacity was represented by dispersal agent (wind-dispersed or non-wind dispersed) and seed mass. To characterize persistence we used lifespan (annual and biannual species classified as short-lived, perennial species classified as long-lived), clonal reproduction (three categories; (1) little or no vegetative spread, (2) shortly creeping, (3) far creeping, cf. Fitter and Peat 1994), and seed bank longevity, using the

**Table 2** Habitat specialists, their national red-list status and their probability of occurrence in response to patch size and patch connectivity

Species	National red list status	No. of occurrences	Response to patch size	Response to patch connectivity
<i>Acinos arvensis</i>	LC	65	0 (0.113)	0 (0.513)
<i>Alchemilla glaucescens</i>	LC	13	0 (0.445)	0 (0.536)
<i>Androsace septentrionalis</i>	NT	16	0 (0.167)	1 (0.033)
<i>Arabis hirsuta</i>	LC	67	0 (0.280)	0 (0.181)
<i>Asplenium ruta-muraria</i>	LC	19	0 (0.344)	0 (0.312)
<i>Avenula pratensis</i>	LC	56	0 (0.740)	0 (0.055)
<i>Carex caryophyllaea</i>	LC	10	0 (0.094)	1 (<0.001)
<i>Carlina vulgaris</i>	NT	18	0 (0.107)	1 (<0.001)
<i>Centaurea scabiosa</i>	LC	14	0 (0.310)	0 (0.069)
<i>Cerastium semidecandrum</i>	LC	15	1 (0.001)	1 (0.003)
<i>Cotoneaster integerrimus</i>	LC	61	0 (0.066)	0 (0.315)
<i>Cotoneaster niger</i>	NT	6	– NA	– NA
<i>Cynoglossum officinale</i>	LC	10	0 (0.143)	1 (<0.001)
<i>Draba verna</i>	LC	17	0 (0.102)	1 (0.040)
<i>Dracocephalum ruyschiana</i>	VU	17	0 (0.781)	0 (0.522)
<i>Echium vulgare</i>	NA	22	0 (0.712)	0 (0.146)
<i>Epipactis atrorubens</i>	LC	1	– NA	– NA
<i>Erysimum strictum</i>	LC	14	0 (0.706)	0 (0.585)
<i>Filipendula vulgaris</i>	NT	68	1 (0.034)	0 (0.911)
<i>Fragaria viridis</i>	LC	67	0 (0.422)	1 (0.047)
<i>Geranium sanguineum</i>	LC	58	1 (0.025)	0 (0.120)
<i>Hypochaeris maculata</i>	LC	17	1 (0.001)	0 (0.102)
<i>Inula salicina</i>	LC	10	0 (0.694)	0 (0.715)
<i>Lappula myosotis</i>	NT	3	– NA	– NA
<i>Lepidium campestre</i>	NA	12	0 (0.712)	0 (0.146)
<i>Ligustrum vulgare</i>	NT	2	– NA	– NA
<i>Linum catharticum</i>	LC	26	1 (0.009)	0 (0.155)
<i>Lithospermum officinale</i>	NT	4	– NA	– NA
<i>Myosotis ramosissima</i>	LC	1	– NA	– NA
<i>Myosotis stricta</i>	LC	2	– NA	– NA
<i>Myosurus minimus</i>	NT	1	– NA	– NA
<i>Odonites vernus</i> ssp. <i>litoralis</i>	VU	2	– NA	– NA
<i>Phleum phleoides</i>	EN	24	0 (0.560)	0 (0.630)
<i>Poa alpina</i> var. <i>alpina</i>	LC	41	1 (0.036)	0 (0.700)
<i>Poa compressa</i>	LC	73	0 (0.143)	0 (0.163)
<i>Polygonatum odoratum</i>	LC	70	0 (0.056)	1 (0.033)
<i>Potentilla crantzii</i>	LC	3	– NA	– NA
<i>Rhamnus catharticus</i>	LC	33	0 (0.469)	0 (0.329)
<i>Rosa majalis</i>	LC	9	– NA	– NA
<i>Saxifraga granulata</i>	LC	6	– NA	– NA
<i>Saxifraga osloënsis</i>	NT	8	– NA	– NA
<i>Saxifraga tridactylites</i>	LC	22	0 (0.087)	1 (0.008)

**Table 2** continued

Species	National red list status	No. of occurrences	Response to patch size		Response to patch connectivity	
<i>Scleranthus perennis</i>	LC	30	0	(0.363)	1	(0.002)
<i>Seseli libanotis</i>	LC	66	0	(0.074)	0	(0.485)
<i>Silene nutans</i>	NT	39	0	(0.234)	0	(0.301)
<i>Sorbus aria</i>	NT	3	–	NA	–	NA
<i>Thymus pulegioides</i>	LC	34	0	(0.155)	0	(0.247)
<i>Veronica arvensis</i>	LC	8	–	NA	–	NA
<i>Veronica spicata</i>	EN	70	0	(0.122)	1	(0.040)
<i>Woodsia alpina</i>	LC	8	–	NA	–	NA
Total			6		11	

Red list categories: *EN* endangered, *VU* vulnerable, *NT* near threatened, *LC* least concern, *NA* not considered for the Norwegian red list

Response = 0 means  $p$  value of parameter estimate  $>0.05$  and response = 1 means  $p < 0.05$ , in a GLMM of probability of occurrence as a function of patch size or patch connectivity (binomial error distribution, patch nested in plot as a random factor).  $p$ -values for each test are included in parenthesis, and the tests were run only for species with  $\geq 10$  occurrences.

seed bank longevity index (Bekker et al. 1998). Trait values were collected from trait databases (Kleyer et al. 2008; Kühn et al. 2004; Fitter and Peat 1994) and the local flora (Lid and Lid 2005). When several records were available in the databases, we used median values for each combination of trait and species.

### Statistical analyses

First we assessed whether plant species richness was related to patch size and connectivity. Due to the spatially structured sampling of habitat patches, with patches nested within  $500 \times 500$  m plots, we used linear mixed effect models, with habitat patch nested within plot as random factor (cf. Zuur et al. 2009). We used maximum likelihood estimation (ML), model simplification and comparison of models using the AIC criterion, and fitted the optimal model using restricted maximum likelihood estimation (REML), as recommended by Zuur et al. (2009). Patch size was  $\log_2$ -transformed to ensure homogeneity of variance and normally distributed residuals. Separate models were run for total plant species richness and for habitat specialist species richness.

Secondly, we investigated the importance of patch size and patch connectivity on the probability of occurrence of habitat specialists. We constructed two separate models for each habitat specialist species occurring in  $\geq 10$  habitat patches. We used generalized linear mixed effect models (GLMMs), with binomial error structure and patch nested within plot as random factor. Presence/absence of the species was used as the response variable. The first model used patch size as predictor variable, and the second model used patch connectivity as predictor variable. Inspection of parameter estimates and  $p$ -values were used to assess whether probability of occurrence was related to patch size or patch connectivity. We did not correct for multiple testing.  $p$ -values for each model are included in Table 2.

We then classified species with a probability of occurrence significantly related to patch size or connectivity as vulnerable to area or isolation and species without such a



relationship as being neutral to area or isolation (Table 2). Then we used generalized linear models (GLMs) to investigate the association between vulnerability to area/isolation and plant traits. Vulnerability to area and isolation were used as response variables in two separate model runs and seed number, dispersal agent, seed mass, lifespan, clonality and seed bank longevity were used as predictor variables. The models were run with a binomial error structure. We used backward model simplification with comparison of AIC-values to guide model selection.

All statistical analyses were carried out in R version 3.0.1 (R Development Core Team 2013), with packages lme4 (Bates et al. 2013) and nlme (Pinheiro et al. 2013).

## Results

A total of 381 vascular plant species were recorded in the 86 habitat patches, of which 50 species were characterized as habitat specialists. There were 26–108 (mean  $\pm$  SD:  $66.9 \pm 21.3$ ) species and the number of habitat specialists varied from 2–30 ( $14.7 \pm 6.0$ ) species per patch. There was a large size range of habitat patches ( $50$ – $9475$  m<sup>2</sup>,  $901.3 \pm 1317.2$  m<sup>2</sup>), and patch connectivity varied from 0.02 to 4.04 ( $1.30 \pm 1.27$ ). Patch size and patch connectivity were positively correlated across the total study area as a whole (Spearman's rank correlation  $r_s = 0.318$ ,  $p = 0.003$ ,  $n = 86$ ), but when taking account of the spatial structure of the data (habitat patches nested within plots), the relationship between habitat patch size and connectivity was weakly negative ( $\beta = -0.037$ ,  $SE = 0.012$ ,  $p = 0.003$ ). This means that for a given patch size, a large variation in connectivity was found across the habitat patches, and vice versa.

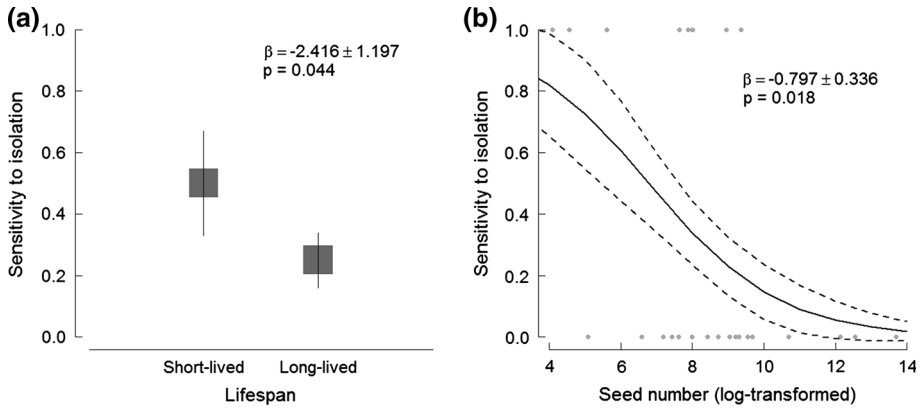
The total species richness was positively related to patch size only ( $\beta = 5.594$ ,  $SE = 1.403$ ,  $p < 0.001$ ), i.e. large habitat patches held higher species richness than small patches. The species richness of habitat specialists was positively related to both patch size ( $\beta = 1.146$ ,  $SE = 0.382$ ,  $p = 0.004$ ) and patch connectivity ( $\beta = 2.153$ ,  $SE = 0.920$ ,  $p = 0.022$ ), i.e. large habitat patches held higher habitat specialist species richness than small patches, and a well-connected habitat patch of a given size was on average more species rich than an isolated patch of the same size.

Of the 50 habitat specialists found in the sample sites, 34 occurred in  $\geq 10$  habitat patches. Of these only six species had a probability of occurrence significantly related to patch size (Table 2). No plant traits could significantly contribute to explaining species vulnerability to habitat patch size (results not shown).

A total of 11 habitat specialist species could be characterized as vulnerable to isolation (Table 2). After model simplification, the best model explaining vulnerability to patch isolation included lifespan ( $\beta = -2.416$ ,  $SE = 1.197$ ,  $p = 0.044$ ) and seed number ( $\beta = -0.797$ ,  $SE = 0.336$ ,  $p = 0.018$ ), with a higher probability for vulnerability in short-lived species and species with low seed number (Fig. 2).

## Discussion

The dry calcareous grasslands in the Oslo fjord area represent a naturally fragmented system of small habitat patches with high conservation value. Human impact, through habitat conversion and degradation, has led to loss of habitat and increased fragmentation in this densely populated area. As expected, the large habitat patches have higher vascular plant species richness, both totally and of habitat specialists, than small patches, reflecting



**Fig. 2** Sensitivity to patch isolation as a function of **a** lifespan (short-lived vs. long-lived) (mean  $\pm$  SE) and **b** seed number (log<sub>2</sub>-transformed) (*dotted lines* represent SE). The parameter estimates of the generalized linear model are shown

the general species-area effect, i.e. an increase in the number of species with the area sampled (Arrhenius 1921; Rosenzweig 1995). Focusing only on habitat specialists we find an additional positive effect of patch connectivity, implying that for a habitat patch of a given size, a well-connected patch will hold more habitat specialists than an isolated patch, in line with findings in calcareous grasslands (Adriaens et al. 2006) and heathlands (Piessens et al. 2004) in Belgium. However, several studies fail to find an effect of present-day patch size or isolation on the richness of habitat specialists in semi-natural grasslands (Krauss et al. 2004; Lindborg and Eriksson 2004; Helm et al. 2006; Cousins et al. 2007). As many plant species are long-lived with the capacity to form remnant populations (Eriksson 1996), a slow response to changes in environmental conditions is expected, at least partly explaining this lack of relationship. This is further supported by a significant relationship between historical landscape configurations and present-day species richness in several studies (Lindborg and Eriksson 2004; Helm et al. 2006; Krauss et al. 2010), which suggests that there may be an extinction debt in these systems. The size of extinction debts can be expected to vary at different spatial scales (Cousins and Vanhoenacker 2011) and will increase with increasing habitat change (Hylander and Ehrlén 2013). It is thus likely that differences in the studied landscapes could contribute to explaining the lack of a consistent relationship between species richness and habitat size and isolation in fragmented grassland (Cousins 2009). Based on a literature review Cousins (2009) suggests that the amount of target habitat remaining in the landscape is a key factor. In landscapes with >10 % of the target habitat remaining the existence of extinction debts is to be expected, and plant species richness should be more strongly related to the historical landscape configuration. In landscapes with <10 % of the target habitat remaining, however, a stronger relationship with present landscape configuration could be expected. The dry calcareous grassland patches in the Oslo fjord area are small (0.005–0.95 ha) compared to other grassland studies (Helm et al. 2006; Cousins et al. 2007; Lindborg 2007; Lindborg et al. 2011) and naturally fragmented, which could explain why we find significant effects of present-day isolation on habitat specialist species richness. In small-scale patches, the populations will be smaller and thus more sensitive to both genetic and stochastic extinctions (Groom 1998). If the inter-patch distance is increased by human land use

changes beyond the dispersal capacity of the specialist species, a further response to increased isolation is to be expected.

About 1/3 of the habitat specialists in our study system show vulnerability to isolation, defined as having lower probability of occurrence in isolated habitat patches. Traits related both to persistence and recolonization ability are predictors of species' vulnerability. Firstly, we find that short-lived species show higher vulnerability to isolation than long-lived species, in line with the theory of remnant population formation (Eriksson 1996). Short-lived plants commonly have large fluctuations in the number of individuals (Matthies et al. 2004) and a high rate of local extinctions (Fischer and Stöcklin 1997), and small, isolated populations can suffer from reproductive failure (Groom 1998). Variability in survival and reproduction has a stronger negative impact on the population growth and stability of short-lived species than long-lived (García et al. 2008; Morris et al. 2008). The empirical evidence of the importance of lifespan in grassland fragmentation studies is inconclusive. Some studies find no vulnerability of short-lived species, suggesting that short-lived species are more dependent on local habitat characteristics (such as rocky outcrops) than of habitat patch size or isolation per se (Adriaens et al. 2006; Lindborg et al. 2011). In our study system the results indicate that the rate of local extinctions is higher for short-lived species in isolated than well-connected patches (Bruun 2000; Lindborg 2007). As we did not assess single-trait relationships with vulnerability to patch isolation and size, but rather assessed the relative importance of the different traits to vulnerability in a multiple regression framework, no effect of the other persistence related traits (clonality, seed bank longevity) was found. Short-lived species are however often non-clonal (Piqueray et al. 2011; Fischer and Stöcklin 1997). A larger sample of species would be necessary to assess the importance of clonality for perennial species.

Secondly, we find that the number of seeds produced per plant is negatively related to vulnerability to isolation, i.e. species with a low seed production have a lower probability of occurrence in isolated habitat patches. Immigration or recolonization can reduce the risk of local extinctions (the rescue-effect; Brown and Kodric-Brown 1977), and modeling studies show that species with low reproductive rate require large amounts of habitat for persistence (Fahrig 2001) and that only species with a high fecundity and long-distance dispersal should be insensitive to habitat loss (Higgins et al. 2003). Seed production has also been found to be an important predictor of vulnerability to fragmentation in urban ruderal habitats (Schleicher et al. 2011) and forest understory herbs (Dupré and Ehrlén 2002). Our results suggest that the increased rates of local extinction (vulnerability of short-lived species) and reduced rates of local recolonization (vulnerability of species with low reproductive output) in combination affects the species richness of habitat specialists, and that mitigation of local, area-dependent extinctions through colonization is reduced in isolated patches.

No traits representing dispersal ability were related to vulnerability to isolation in our study system. Theoretical and empirical studies underline the importance of both mean dispersal range and the number of potential dispersers (Higgins et al. 2003; Schleicher et al. 2011). Terminal velocity is suggested as a relevant and easily measured trait for dispersal range (Schleicher et al. 2011), but due to several missing values in our dataset we did not include terminal velocity in the analyses. Instead we included seed mass and dispersal mode (wind- versus not wind-dispersed), which might have been too crude measures of interspecific differences in mean dispersal range. Dispersal mode was also found to be a poor predictor of vulnerability to isolation in Danish grasslands (Bruun 2000). A more detailed investigation of dispersal distances and how dispersal vectors

interact with habitat fragmentation is warranted in order to understand how species are limited by migration in a fragmented landscape (Higgins et al. 2003).

## Conclusions

Species predicted to show the fastest response to environmental change also have lowest persistence in the fragmented landscape of dry calcareous grasslands in the Oslo fjord area, suggesting that landscape structure indeed affects species richness in our study system. Being more species rich, conservation of the large habitat patches is an important prerequisite for protection of vascular plant biodiversity. The additional effect of connectivity, i.e. that isolated patches hold lower habitat specialist species richness than non-isolated patches of a given size, implies that maintaining well-connected, large habitat patches should be a management priority in this region.

Our findings support the recent international efforts within “connectivity conservation management” (cf. Worboys et al. 2010), which focus on the maintenance and restoration of connectivity of core areas of habitat. In order to maintain biodiversity patterns and ecological processes in the landscape, more attention should be given to the spatial configuration of habitat networks (Franklin and Lindenmayer 2009), and on the preservation of colonization processes to ensure regional persistence of species.

This is especially important for the most vulnerable species, like specialist species (several included on the national red list) associated with rare habitats in high-pressure areas. The dry calcareous grasslands in the Oslo fjord, along with scores of other areas of high biodiversity value around the world, occur in an area of several conflicting interests, including urban development and human recreation. Careful spatial considerations—combined with integrated cross-sector collaboration between conservation managers and urban planners—can improve the chance of long-time persistence of the biodiversity values also in high-pressure areas.

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