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Abstract

We examined the response of vascular plant species richness to long-term habitat loss and fragmentation of Estonian calcareous grasslands (alvars). The current number of habitat specialist species in 35 alvars was not explained by their current areas and connectivities but it was explained by their areas and connectivities 70 years ago ($R^2 = 0.27$). We estimated the magnitude of extinction debt in local communities by assuming an equilibrium species richness in 14 alvars that had lost only a small amount of area and by applying this model to the remaining alvars, in which the average area has declined from 3.64 km$^2$ in the 1930s to 0.21 km$^2$ at present. The extinction debt estimated for individual alvars was around 40% of their current species number. Our conclusions are applicable to temperate grasslands in general, which have lost much area because of agricultural intensification and cessation of traditional management.

Keywords

Connectivity, extinction debt, fragmentation, grassland plants, metapopulation dynamics, species–area relationship, species richness, transient time.


INTRODUCTION

Habitat loss is the primary environmental cause of biodiversity decline at local, regional and global scales (Dirzo & Raven 2003; Balmford et al. 2005). It is more controversial to what extent fragmentation of habitats has an influence on the dynamics of biodiversity independently of the loss of pooled habitat area. Many researchers have concluded that habitat fragmentation poses an important additional threat to biodiversity (Hanski 2005; Piessens et al. 2005; Strantford & Robinson 2005), but others think that fragmentation per se is generally of secondary importance (Fahrig 2003). The latter conclusion has been supported by empirical studies that have failed to demonstrate a significant effect of connectivity (and hence of fragmentation) on the occurrence of species in fragmented landscapes (see references in Fahrig 2003).

One reason why the effect of connectivity might not be significant in empirical studies is slow response of populations to environmental changes (Hanski 2005). Hanski & Ovaskainen (2002) examined the response of metapopulations to habitat loss and fragmentation with a model. They showed that the transient time during which the metapopulation is approaching the new (quasi-)equilibrium following environmental change is especially long when the new equilibrium is located close to the extinction threshold, which gives the minimum amount and respective configuration of habitat that is necessary for long-term persistence. Such slow (meta)population responses create an extinction debt in communities (Tilman et al. 1994; Hanski 2000): following environmental change, populations and metapopulations are present, although in declining numbers, for shorter or longer periods of time, even if they are expected to go ‘deterministically’ extinct.

Here, we examine the occurrence of habitat specialist plant species in a fragmented landscape in Estonia. The landscape consists of calcareous dry grasslands with thin soil on limestone bedrock, called alvars, which are characterized by high species richness of plants both at small scales and at the community level (Pärtel et al. 1999a). Alvar grasslands occur as distinctive patches within the surrounding landscape, and the specialist species comprise a characteristic metacommunity (Leibold et al. 2004).

Studying the alvar grasslands in Estonia, Pärtel & Zobel (1999) found no relationship between the area of a habitat patch and species number. One possible reason for this unexpected result is the dramatic decline in the area of alvar grasslands since the 1930s as the result of changes in land
use and consequent non-equilibrium state in the plant communities. Following the abandonment of grazing alvars have started to overgrow with bushes (mostly Juniperus communis) and trees (mostly Pinus sylvestris; Partel et al. 1999b). Similar losses of grasslands have occurred across northern Europe (Eriksson et al. 2002; Luoto et al. 2003).

The aims of this study are to investigate to what extent the species richness of alvar grassland plant communities is related to the past and current areas and spatial connectivities of the habitat patches, and to estimate the magnitude of possible extinction debt in this community because of habitat loss and fragmentation.

**MATERIALS AND METHODS**

We studied the vascular plant species occurring on alvar grasslands of two large Estonian islands, Saaremaa and Muhu (Fig. 1). These islands are located in the Baltic Sea, west of the Estonian mainland (c. 58° N, 22–23° E). The area of the two islands is 2900 km², the mean annual temperature is 6 °C, and the mean annual precipitation is 600–650 mm (Raukas 1995).

In July 2001, we selected 35 characteristic alvar grassland patches and counted all vascular plant species within a circle area with the radius of 30 m. The areas of the study patches varied from 1 to 340 ha (total area 16 km²). Amongst all the species recorded, there were 84 alvar specialist species (Helm 2003) to which this analysis is restricted.

To determine the past areas and connectivities of the alvar grasslands, we used detailed maps of Estonian vegetation cover for the 1930s (1 : 200 000; Laasimer 1965, Fig. 1a). The situation in the 1930s is thought to correspond to the state of alvar grasslands that persisted for centuries (Pärtel et al. 1999b). To measure the current areas and connectivities, we used recent maps of “The inventory of Estonian seminatural communities 2000”, produced by Estonian Fund of Nature and Estonian Seminatural Community Conservation Association (Fig. 1b).

**Connectivity of alvar patch** $i$ was calculated with the formula (Hanski 1994; Moilanen & Nieminen 2002, Eq. 3):

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

where $A_j$ is the area of patch $j$ (ha), $d_{ij}$ is the distance (km) between the centroids of patches $i$ and $j$, and $\alpha$ is the parameter of the exponential distribution setting the influence of distance on connectivity. We used centroid-to-centroid distance because the study patches are relatively small compared with the scale of the landscape. We used $\alpha = 0.34$, which corresponds to average migration distance of 3 km. This is a realistic migration range for many alvar grassland species that used to be dispersed by sheep herded from one pasture to another (Bruun & Fritzbøger 2002; Franzen & Eriksson 2003). In any case, the results are not very sensitive to the value of $\alpha$ (Moilanen & Nieminen 2002). We used linear multiple regressions to relate the current species number to the current and past (log-transformed) areas and connectivities of the alvars (two separate models for past and current landscape structures).

To estimate the magnitude of the extinction debt – the number of extinctions yet to happen – we used the following approach. We identified 14 alvar grasslands in which the ratio of the current area to past area was at least 0.20. The average amount of retained area in these grasslands was 41%, whereas in the remaining 21 grasslands it was only 6%. We constructed two separate multiple regression models for these 14 more stable alvars, in which the current species number was explained either by the current areas and connectivities or by the past areas and connectivities. The assumption here is that species richness has remained relatively stable in these patches, because the patches themselves have lost relatively little area. This assumption was supported by a significant species–area relationship with both past and current patch areas (z of the logarithmic species–area relationship was 0.15 and 0.10 respectively). Also, Cousins et al. (2003) found for Swedish grasslands that most extinctions occur when the remaining

**Figure 1** Maps of the extent of alvar grasslands in the Estonian islands of Saaremaa and Muhu. (a) The distribution of alvars in the 1930s, before the rapid decline in their area. (b) The current distribution of alvars (in the year 2000).
area is below 10–30%. We then used the regression models thus obtained to predict the species number in the 21 patches that had lost much area (and connectivity), using their current areas and connectivities as the explanatory variables. The extinction debt is given by the excess of observed species in comparison with the predicted number of species: (observed number−predicted number)/observed number. The two models bracket the magnitude of the extinction debt: the model based on past landscape structure probably gives an overestimate (because some of the original species may have been lost from the stable reference grasslands), while the model based on the current landscape probably gives an underestimate (because there may exist some extinction debt also in the reference grasslands).

RESULTS

In the 1930s, there were 377 alvar grassland patches in Saaremaa and Muhu, covering an area of 260 km² (Fig. 1a). Average connectivity ($\bar{x}$) was 3.78 ($\pm$ 2.43 SD). By the year 2000, the total area of alvars had declined to 78 km² (Fig. 1b). However, because of widespread fragmentation of previously extensive grasslands, the total number of distinct patches had increased to 413. Average connectivity had declined to 1.34 ($\pm$ 0.82).

Current areas and connectivities of the alvars explained no variation in the current number of alvar specialist plant species in the 35 alvars (Table 1). In contrast, past areas and connectivities both had a significant positive effect on the current number of species (Fig. 2). A multiple regression model including both past area and past connectivity explained 27% of variation in the current species number (Table 1).

We calculated comparable regression models for the generalist plant species ($n = 88$) that occur also or primarily in other habitats than alvars. In this case past landscape structure and current connectivity had non-significant effects on current species number, while the species number was negatively related to current area ($R^2 = 0.23$, $P = 0.002$). The latter result is probably because of the large perimeter to area ratio in small alvars, making it more likely that species present in the surrounding habitats disperse to an alvar.

Considering multiple regression models for the 14 more stable grasslands, which had retained 41% of their past area on average, the model with current areas and connectivities explained 26% of variation in the number of specialist species ($P = 0.07$), while the respective model with past areas and connectivities explained 44% of variation in species number ($P = 0.02$). We applied these models to predict species number in the remaining 21 patches that had lost most of their area. The model based on past landscape structure predicted an extinction debt of 43% on average, while the model constructed with current areas and connectivities predicted that the alvars have an extinction debt of 11% on average. The former estimate is more realistic, because we do not expect that the 14 reference alvars have lost a large fraction of their species. Assuming this model, and based on the 95% CI for the predicted numbers in individual alvars, we calculated a rough 95% CI of 17–70% for the 43% extinction debt estimate. This is the predicted level of extinction debt in 21 alvar grasslands that used to be 3.64 km² in size on average in the 1930s but are only 0.21 km² on average at present.

DISCUSSION

Over the past century, grasslands and other seminatural plant communities in temperate Europe have suffered dramatic decline in their area due to land-use changes, and thereby once widespread vegetation types have become highly vulnerable (Luoto et al. 2003). But what we have lost in area we may still have in species richness. Many grassland plant species with long life cycles, slow intrinsic dynamics and relatively large populations appear to occur as remnant populations and communities in modern landscapes (Eriksson 1996; Fischer & Stöcklin 1997; Eriksson 2000; Maurer et al. 2003). Given the biological traits of the species, it may take a substantial length of time before the adverse consequences of habitat loss and fragmentation become apparent in terms of greatly reduced local and regional species richnesses.

Our results strongly support the notion of remnant grassland plant communities with a slow response to environmental change. Current species richness in fragmented alvar grasslands was not related to the current areas and connectivities of the habitat patches, but it was significantly related to their past areas and connectivities, i.e., to the state of the landscape prior to drastic habitat loss and fragmentation. These results clearly point to the existence of

**Table 1** Multiple regression models for the effects of past area and past connectivity ($n = 35$, $F_{2,32} = 7.34$, adjusted $R^2 = 0.27$, $P = 0.002$) and for the effects of current area and current connectivity ($n = 35$, $F_{2,32} = 0.74$, adjusted $R^2 < 0.001$, $P = 0.48$) on the current species richness of alvar specialist plant species

<table>
<thead>
<tr>
<th>Variable</th>
<th>$B$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>40.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Past area</td>
<td>7.1</td>
<td>0.013</td>
</tr>
<tr>
<td>Past connectivity</td>
<td>1.1</td>
<td>0.010</td>
</tr>
<tr>
<td>Intercept</td>
<td>45.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Current area</td>
<td>1.1</td>
<td>0.526</td>
</tr>
<tr>
<td>Current connectivity</td>
<td>1.6</td>
<td>0.247</td>
</tr>
</tbody>
</table>

Area was log-transformed. See Fig. 2.
extinction debt – a slow response of populations that eventually go extinct because of habitat destruction (Tilman et al. 1994; Hanski & Ovaskainen 2002). Alvar grasslands in Estonia had been relatively stable for centuries (Poska & Saarse 2002), but during the past 50 years they have lost 70% of their area due to cessation of traditional management. Assuming that species richness has remained approximately at equilibrium in those patches that have suffered little reduction in area, we estimated the magnitude of extinction debt at around 40% in individual alvars, corresponding to predicted loss of around 20 vascular plant species per alvar in the future. With current landscape structure, many of these species will be lost from the entire region, although this will be an even slower process than extinction from individual alvars.

Long transient times in population and metapopulation extinction have been demonstrated with a variety of data and methods for: (i) a wide range of terrestrial and freshwater taxa in Singapore (Brook et al. 2003); (ii) tropical birds in forest fragments in Kenya (Brooks et al. 1999); (iii) primates in African forests (Cowlishaw 1999); (iv) old-growth specialist beetle species in Finland (Hanski 2000); and (v) epiphytic lichens in boreal Sweden (Berglund & Jonsson 2005). Pykälä et al. (2005) studied abandoned seminatural grasslands and found rare plant species to be rather resistant to the cessation of grazing and abandonment of grassland.

Apart from slow response of communities to lost area, a corresponding response to decreasing connectivity has been shown to lead to extinction debt. Thus Lindborg & Eriksson (2004) found that the current species richness of Swedish seminatural grasslands is related to the connectivity of the sites 50–100 years ago, although species richness was not related to the historical areas of their study sites. In Belgian heathlands, Piessens et al. (2004, 2005) showed that the isolation of habitat fragments was more important in explaining species richness and community composition than fragment area. These results indicate the presence of the rescue-effect (Brown & Kodric-Brown 1977), which allows populations to persist with a high probability even in small habitat patches if they are well connected. In our results, both area and spatial connectivity 70 years ago had a significant effect on current species number. That both of these variables had a significant effect is probably explained by our data coming from a thoroughly mapped large area with much variation in habitat patch areas and connectivities. In a study of woodland plants in a slowly changing landscape in the UK, Verheyen et al. (2004) were able to demonstrate clear effects of both woodland area and connectivity on the presence of especially those species with low seed production and predominantly short-range seed dispersal. Such species are expected to respond especially slowly to environmental change.

Thorough enumeration of all plants within a large number of large habitat patches is not possible; in our case the pooled area of the 35 study alvars was 16 km². We characterized local species richness with the number of species recorded within circular sample plots with the radius of 30 m. According to the species pool concept (Pärtel et al. 1996), a sample plot with fixed size will
include a constant proportion of species in the entire area, and equally large sample plots should reflect the effect of area independent on habitat diversity (Köchy & Rydin 1997). Several studies (Kelly et al. 1989; Köchy & Rydin 1997; Krauss et al. 2004) have, however, not detected a significant species–area relationship while using sample plots with fixed size, but the reason may be the same as in our case. There was no relationship between current species number and current habitat area, although there was a strong relationship between current species number and past habitat area.

The slow response of populations and metapopulations to habitat loss and fragmentation has important implications for conservation. Recording current species number without considering the extinctions yet to happen because of past environmental changes will lead to overestimation of long-term species richness and corresponding underestimation of their level of threat (Hanski & Ovaskainen 2002). Knowing that species richness is eventually dependent on area and connectivity leads to predicted future extinctions, but the transient time in species’s responses also provides an opportunity for conservation. What is required is active and well-informed management, involving strategic habitat restoration and activities that facilitate dispersal among sites (Fischer et al. 1996; Bruun & Fritzboeger 2002; Znamenskiy et al. 2005). But first of all conservation agencies must take the extinction debt seriously in their planning. The key message is that urgency to take action now is even greater than one might expect based on even the most up-to-date red data books.

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REFERENCES


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