DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
126

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126

# FORMATION AND PERSISTENCE OF DRY GRASSLAND DIVERSITY: ROLE OF HUMAN HISTORY AND LANDSCAPE STRUCTURE

## AVELIINA HELM

TARTU UNIVERSITY
PRESS

Institute of Botany and Ecology, University of Tartu, Tartu, Estonia

The dissertation is accepted for the commencement of the degree of *Doctor philosophiae* in botany at the University of Tartu on March 28, 2007 by the Doctoral committee of the Faculty of Biology and Geography of the University of Tartu.

Supervisor: Prof. Meelis Pärtel

Opponent: Dr. Olivier Honnay (Laboratory of Plant Ecology,
University of Leuven)

Commencement: Room 218, Lai 40, Tartu, on May 29, 2007, at 10.15

The publication of this dissertation is granted by the Institute of Botany and Ecology, University of Tartu.

ISSN 1024–6479
ISBN 978–9949–11–592–1 (trükis)
ISBN 978–9949–11–593–8 (PDF)

Tartu Ülikooli Kirjastus
www.tyk.ee
Tellimus nr 159

# CONTENTS

# LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals:

I Helm, A., Hanski, I. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters,* 9, 72–77.

II Pärtel, M., Helm, A., Reitalu, T., Liira, J. & Zobel, M. (2007) Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology,* 95, 574–582.

III Znamenskiy, S., Helm, A. & Pärtel, M. (2006) Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. *Biodiversity and Conservation,* 15, 1797–1809.

IV Pärtel, M. & Helm, A. (2007) Invasion of woody species into temperate grasslands: Relationship with abiotic and biotic soil resource heterogeneity. *Journal of Vegetation Science,* 18, 63–70.

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The participation of the author in preparing the listed publications is as follows: 90% (paper I), 50% (paper II), 50% (paper III), 60% (paper IV).

# INTRODUCTION

Semi-natural grasslands are among the most species rich vegetation types in Europe and possess great conservational value (Eriksson *et al.* 2002; Poschlod & WallisDeVries 2002; Sutherland 2002; WallisDeVries *et al.* 2002). In this thesis, I studied the formation and persistence of biodiversity in semi-natural calcareous grasslands, known as alvars. European alvars occur along a narrow zone of Ordovician and Silurian limestone on the southern edge of the Baltic crystalline shield. This belt starts in SE Sweden, extends through the islands of Öland, Gotland, Saaremaa, Hiiumaa and Muhu, coastal parts of the Estonian mainland and ends in NW Russia, in the Izhora plateau near the southern coast of Lake Ladoga. Alvar grasslands form rather distinctive patches within the surrounding landscape, thus the specialist species comprise a characteristic metacommunity (Leibold *et al.* 2004). Alvars have an anthropogenic origin and in the case of cessation of traditional management e.g. grazing and mowing, alvars, as well as other semi-natural grasslands, overgrow with shrubs and trees, resulting in habitat loss and fragmentation (Pärtel *et al.* 1999a; Rosén & van der Maarel 2000). Alvars in Estonia have declined from around 50 000 hectares in the1930s to only 10 000 hectares in 2000 (Kukk & Sammul 2006).

Alvars are characterized by a high number of vascular plant species both on a small scale and at the community level (Pärtel *et al.* 1999b), but species richness may vary greatly even between apparently similar habitat patches. The objective of this thesis was to search for the causes of variation in species richness and to determine the underlying processes in overgrowing of semi-natural grasslands.

There have been several attempts to reveal the mechanisms behind formation and persistence of species diversity in plant communities, but some aspects remain almost unnoticed. Generally speaking, species diversity in a local community is an equilibrium between the arrival of new species and the number of local extinctions (MacArthur & Wilson 1967). The potential number of arriving species depends on the size of the species pool (Pärtel *et al.* 1996; Zobel 1997), which is determined by large-scale processes such as evolution and historical migration of species (Ricklefs 1987; Pärtel 2002). Species arrival to a local community and their persistence at any particular site depends on the proximity of potential seed sources (i.e. connectivity of the given habitat) (Bruun 2000; Matlack 2005), the presence of dispersal vectors (Ozinga *et al.* 2004; Poschlod *et al.* 1998) and the permeability of matrix landscape (Zobel *et al.* 2006). Extinctions in a local community take place when the habitat quality decreases, area shrinks and – in case of semi-natural communities – the management conditions change (Fischer & Stöcklin 1997).

Habitat loss and fragmentation is the primary environmental cause of declining biodiversity on local, regional, and global scales (see references in paper **I**). Nevertheless, empirical studies have often failed to demonstrate the significant effect of connectivity (and hence the fragmentation) and habitat area on the number of species in fragmented landscapes (see references in Fahrig 2003). One possible reason for these unexpected results is the dramatic decline in the area and connectivity of studied systems and consequent non-equilibrium state of the plant communities. Many species may have a delayed response to environmental changes (i.e. habitat loss and fragmentation) due to slow intrinsic dynamics of populations. This creates an extinction debt in communities. Extinction debt is 'a future ecological cost of current habitat destruction' (Tilman *et al.* 1994, p. 65), which leads to loss of species after a prolonged transient time following habitat destruction (Hanski 2000, 2005). Due to rapid decrease in area and connectivity in past 70 years, alvars in Estonia may act as remnant plant communities and have a delayed response to environmental change. I hypothesize that, due to possible extinction debt in our alvar communities, the current species richness is characterized by the past area and connectivity of alvars rather than the current area and connectivity.

Semi-natural grasslands represent ecosystems that have developed and endured due to historical and current human impact e.g. animal husbandry, mowing and gathering of firewood, but the historical factors potentially affecting species diversity have often been overlooked. The formation of alvars in Estonia dates back thousands of years (Poska *et al.* 2004). Distribution of semi-natural grasslands increased rapidly during the Roman Era due to the introduction of agricultural activities, and these grasslands have become especially widespread since the Middle Ages (Poska *et al.* 2004). Currently observed alvars have persisted for centuries under constant conditions, as it takes long and stable management for high species richness to form in semi-natural communities (Cousins & Eriksson 2002). Though the area of calcareous grasslands has decreased greatly during the past 70 years, it would still be possible to recognize the species richness that originates from past as these communities may suffer the extinction debt. I hypothesize that high human population density since the Late Iron Age (ca 1000 years ago) has enhanced the dispersal and persistence of many grassland species and has therefore had a positive effect on species richness. Currently very species-rich alvar grasslands are hypothesized to occur only in places where there has historically been enough inhabitants maintaining sufficient amount of grazing animals.

Management history (grazing animals and herding sheep and cattle from one pasture to another or to the market) plays an important role in the formation of species composition of semi-natural communities due to the effect on dispersal of diaspores (Poschlod *et al.* 1998). Near St. Petersburg there are several outcrops of Ordovician limestone, but the presence of alvars in the NW Russia has remained unnoticed though alvars are well known and have been studied for decades in Sweden and Estonia (see references in paper **III**). St. Petersburg was founded in 1703 by Peter the Great. Each year 20 000 workers were recruited to build the city (Dukes 1997, p. 85). The population of the city reached 40 000 by the 1720s and was increasing rapidly (Matley 1981). As everyone had to be supplied with food, wool and dairy products, much livestock was herded from Estonia to the market near St. Petersburg (Moora 1964). My objective was to find out whether the meadows on limestone openings near St. Petersburg belong to alvar vegetation type and whether the historical connection between northern Estonian alvars and NW Russian pastures have resulted in similarities in their species composition.

Changes in management conditions have a direct effect on the number of extinctions in semi-natural grasslands. Due to abandonment of alvars, trees and shrubs quickly invade the community. In order to understand the mechanisms of grassland overgrowth we need to understand the ecology of herbaceous and woody life forms (Wilson 1998). The invasion of woody species into grasslands is often related to soil resource levels and soil heterogeneity – in temperate regions, woodlands are more commonly found on heterogeneous soils and grasslands on homogeneous soils (Pärtel *et al.* 2007). Although the invasion of woody species into semi-natural grasslands has caused much concern, the interplay with soil resource levels and heterogeneity has not been considered. Grassland species may be much more effective in soil resource acquisition than woodland species if the resources are low and homogenously distributed. Most Estonian alvar grasslands currently lack management, but some sites are more overgrown than others (Pärtel *et al.* 1999b). This may be explained by abiotically low and homogeneous soil resource levels that are unfavourable for woody species.

The objectives of this thesis were:

1. to investigate how the current species richness of alvar grassland plant communities relates to the historical and current landscape structure and if the effect of historical processes on current species richness dates back as far as the Late Iron Age (**I**, **II**);
2. to estimate the magnitude of possible extinction debt in alvar grasslands due to recent habitat loss and fragmentation (**I**);
3. to determine the species composition of isolated alvar communities in Izhora plateau, NW Russia as an example of the importance of human enhancement of historical species dispersal (**III**);
4. to ascertain whether the habitat loss due to invasion of woody species is related to soil characteristics of alvar grasslands (**IV**).

# MATERIAL AND METHODS

In all papers the study objects were dry calcareous grasslands, representing *Avenetum* type alvar communities (Albertson 1950; Pärtel *et al.* 1999b). Calcareous grasslands occur in areas where Ordovician or Silurian limestone bedrock is covered by only a thin layer of weathered material. The soil type is rendzic leptosol and the humus layer is 2–25 cm thick (Pärtel *et al.* 1999b).

Except for paper **II**, where the fieldwork was done on the Izhora plateau in NW Russia, the studies were carried out in Estonia – a northern European country on the eastern shore of the Baltic Sea (58–60ºN, 22–28ºE). The vegetation of Estonia belongs to the boreo-nemoral zone (Sjörs 1965). Calcareous grasslands are found mainly in the western and northern part of Estonia, where the climate is relatively maritime; the annual precipitation is 500–700 mm and the mean temperature is 17ºC in July and –5ºC in January (Raukas 1995).

## Paper I

The field studies were carried out on 35 characteristic alvar grassland patches on the western-Estonian islands of Saaremaa and Muhu. All vascular plant species were counted within a circle with 30 m radius. Only characteristic alvar species were included to analysis (for the list of species, see Helm 2003). To determine the past areas and connectivities of the alvar grasslands, I used detailed maps of Estonian vegetation cover from the 1930s (1:200000; Laasimer 1965; Paper **I**, Fig. 1a). The situation in the 1930s is thought to correspond to the original distribution of alvar grasslands that had endured for centuries (Pärtel *et al.* 1999a). To obtain current areas and connectivities, I used recent maps of Estonian semi-natural communities produced by the Estonian Seminatural Community Conservation Association (**I**, Fig. 1b) in 2000.

Connectivity of alvar patch *i* was calculated by the formula from Moilanen and Nieminen (2002):

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

where $A_j$ is the area of grassland 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 (average migration radius = $1 / \alpha$). Here I used $\alpha = 0.34$, which corresponds to an average migration distance of 3 km.

I used linear multiple regression 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 I 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 it was only 6% in the remaining 21 grasslands. I constructed two separate multiple regression models for these 14 more stable alvars, in which the current species number was accounted for either by the current areas and connectivities or by the past areas and connectivities. Then I used these regression models 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 # – predicted #)/observed #.

## Paper II

Forty-five calcareous grasslands were included in the study (**II**, Fig. 2). Detailed descriptions of these study sites are found in Pärtel *et al.* (1999b). Each stand was described by 15 randomly located sample plots of 1m$^2$, in which the presence of all vascular plants was recorded. Large-scale plant diversity was denoted by the size of the community species pool, which was compiled from 15 sample plots within a stand as cumulative species list. Only the characteristic alvar species were included in the analysis (for the list of species, see Pärtel *et al.* 1999b)

I quantified relative human population densities during the Late Iron Age for each study site dependent on their distance from Late Iron Age fortresses and villages (**II**, Fig. 2a), using the same formula of Moilanen and Nieminen (2002) as in paper **I**:

$$\textit{Historical relative human population density} = \Sigma \exp(-\alpha d_i)A_i$$

The summation included all settlement points; $d_i$ is the distance in kilometres between a grassland patch and settlement point $i$ with relative size $A_i$ (1 for a fortress and 0.01 for a minor settlement). Here I set α to 0.1 (analogous to 10 km).

In addition to historical human population density I also considered the effect of current population densities (**II**, Fig. 2b) obtained from the official population census in 1999 from Statistics Estonia (www.stat.ee). Variables that may affect plant diversity were incorporated in the analysis as follows: (1) grassland area in the 1930s, (2) connectivity to other similar grasslands in 1930s, (3) elevation above sea level. Twenty soil samples were collected and analyzed for (4) pH, (5) total N content and (6) P content. In addition, (7) mean soil depth, (8) soil heterogeneity as the coefficient of variation of the soil depth, (9) geographic east-west gradient and (10) precipitation were included.

A General Linear Mixed Model (Littell *et al.* 1996) was used to generate models with different plant diversity parameters. From all models I chose the optimal according to the Akaike Information Criterion (AIC, Akaike 1973). In spatial studies, it is also important to take into account the effect of spatial autocorrelation as nearby points in space tend to have more similar values than would be expected by chance. For that I used a spatial correlation setting that included a distance-dependent covariance matrix in the model and adjusted the test statistics accordingly (Evans *et al.* 2006).

## Paper III

The field studies were carried out at five sites on the Izhora limestone plateau on the territory of Dontso Natural Monument in the Volosovo district of Leningrad oblast (**III**, Fig. 1). Herbaceous vascular plant species were recorded from 15 randomly located 1m$^2$ sample plots. Community species pools were compiled from 15 sample plots within a stand as cumulative species lists. Obtained data were compared with the similar data from Estonian alvars (for the description of study sites, see Pärtel *et al.* 1999b) by using Outlier Analysis and Cluster Dendrogram Analysis.

## Paper IV

Fieldwork was carried out in 26 sites, from which I sampled an open alvar grassland and adjacent former grassland now overgrown by a 30-year-old pine (*Pinus sylvestris* L.) forest. Historical borders of grasslands were obtained from the same map as in papers **I** and **II**.

In August 2003 I measured soil depth, moisture, nutrient content and root parameters in central areas of paired grasslands and forests. I used 1 m linear transects of 11 samples, with a distance of 10 cm between samples (altogether 572 samples for both soil and roots). Root and soil measurements to a depth of 3 cm were taken as close as possible to each other (1–2 cm). Soil volumetric moisture content was measured with a ThetaProbe (Delta-T Devices Ltd., UK). Soil nutrient status was characterised by organic matter content, which was determined by loss-on-ignition. One sample for soil total nitrogen was taken from all forests and grasslands.

I determined root parameters from soil cores 3 cm deep and 0.7 cm in diameter (~1 cm$^3$).

I applied the *t*-tests for dependent samples to compare the same soil and root parameters in paired grasslands and forests.

# RESULTS

In the 1930s alvar grassland patches in Saaremaa and Muhu covered an area of 260 km$^2$ (**I**, Fig. 1a). Average connectivity (Si) was 3.78 (± 2.43 SD). By 2000, the total area of alvars had declined to 78 km$^2$ (**I**, Fig. 1b) and average connectivity had declined to 1.34 (± 0.82). The model considering original (historical) alvar habitat area and original connectivity 70 years ago described 27% of the variation in the current number of characteristic alvar plant species in the 35 alvars. In contrast, current areas and connectivities of the alvars explained no variation in current species number (**I**, Fig. 2, Table 1). Although there has been massive loss in area and connectivity, current species richness corresponds to historical landscape structure and due to extinction debt, it has not yet achieved a new equilibrium state. 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 ($P = 0.07$), whereas the respective model with past areas and connectivities explained 44% of variation in species number ($P = 0.02$). I 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 average extinction debt of 43%, whereas the model constructed with current areas and connectivities predicted that the alvars would average an extinction debt of 11%. The former estimate is more realistic, because I do not expect the 14 reference alvars to have lost a large fraction of their species. Assuming this model, and based on the 95% confidence intervals for the predicted numbers in individual alvars, I calculated a rough 95% confidence interval of 17 to 70% for the 43% extinction debt estimate.

In addition, the current community species pool of the 45 dry calcareous alvar grasslands showed a positive linear correlation with the Late Iron Age human population density (**II**, Fig. 3, Table 1). In the model constructed in paper **II**, two additional factors had significant non-linear effects on the size of large-scale species richness: elevation, indicative of the age of the plant community, and soil N content (**II**, Fig. 3, Table 1). In the second model, small-scale species richness had a significant unimodal relation with current human population density and with elevation above sea level and a linear relationship with historical connectivity to other similar grasslands and with Late Iron Age human population density (**II**, Fig. 4, Table 1). Spatial autocorrelation was significant in both models.

Geographically isolated calcareous alvar grasslands in NW Russia do not differ in their vegetation composition from alvar grasslands in Estonia (**III**, Fig. 2). Cluster Dendrogram Analysis (**III**, Fig. 3) showed that alvar grasslands on the Izhora plateau (Cluster 8) belong to the same group as Estonian *Avenetum*-type alvars, being most similar to the alvars in northern Estonia (Cluster 7).

Overgrowing of alvar grasslands with trees and shrubs is associated with changes in soil characteristics. Soils of overgrown alvars are much more heterogeneous and have significantly deeper maximal soil depth than open grasslands (**IV**, Fig. 1). In addition, roots of woody species are much more patchily distributed (**IV**, Fig. 2).

# DISCUSSION

Current species richness in highly-fragmented dry grassland communities depends on historical factors, although possible effects of past events on current habitat characteristics have often been overlooked by plant ecologists (Briggs *et al.* 2006). I found that both historical landscape configuration (**I**, Fig. 2) and human population density 1000 years ago (**II**, Fig. 3) have a strong effect on the current species diversity of recently fragmented calcareous dry grasslands.

Throughout the last millennium the distribution of calcareous grasslands in Estonia was relatively stable (Poska & Saarse 2002), but over the past century, grasslands and other semi-natural plant communities in Estonia, as well as all over temperate Europe, have suffered a dramatic decline in their area due to changes in land-use. Previously widespread vegetation types have become highly vulnerable (Luoto *et al.* 2003). The area of alvars in Estonia has decreased by five times since 1930s. This magnitude of loss should lead to a decrease in diversity, as a relationship between the area of habitat and species richness is generally considered a rule (Lomolino 2000). Nevertheless, many grassland plant species with long life cycles and slow intrinsic dynamics may occur in modern landscapes, forming remnant populations and communities (Eriksson 1996; Fischer & Stöcklin 1997; Eriksson 2000; Maurer *et al.* 2003; Lindborg & Eriksson 2004; Lindborg *et al.* 2005). I found that current species diversity in fragmented alvar grasslands was not related to the current areas and connectivities of the habitat patches, but was related to their past areas and connectivities, that is, to the state of the landscape prior to drastic habitat loss and fragmentation (**I**, Fig. 2). This means that species composition and diversity have long development times and long 'memory'. In addition to Estonian alvars, extinction debt for plants is also shown to exist, for example, in remnants of traditionally managed seminatural grasslands in Sweden (Lindborg & Eriksson 2004), in forest fragments in Vlaams-Brabant (Vellend *et al.* 2006), but not in fragmented calcareous grasslands in southern Belgium (Adriaens *et al.* 2006).

But how far does the effect on current species richness extend back in time? European semi-natural grasslands developed under human influence and were kept open by grazing, mowing and gathering of firewood. Palynological records combined with archaeological data from northern Estonia show high diversity of grassland species and increasing and constant animal husbandry since 2000 BC (Poska *et al.* 2004). During the Late Iron Age (ca 1000 years ago) the entire Baltic Sea region was densely populated, grasslands were common, and palynological records indicate a high diversity of grassland species (Enckell *et al.* 1979; Lindbladh 1999; Poska & Saarse 2002).

I hypothesized that species diversity of calcareous grasslands is positively dependent on human population density thousand years ago. Indeed I found that both the size of the community species pool and small-scale species diversity are significantly positively correlated to the Late Iron Age human settlement density (**II**, Fig. 3, 4). For the first time I showed that high prehistoric human population density coincides with high current plant diversity in semi-natural grasslands. Thus, relatively continuous land-use and enhancement of plant dispersal have most likely contributed to the diversity patterns that we can observe today. I also considered several other parameters that have been related to plant species richness in semi-natural grasslands. Elevation above sea level, historical connectivity to other similar grasslands, soil N content, current human population density and spatial autocorrelation were significant in the models (**II**, Fig. 3, 4). The size of the community species pool was greatest in plant communities of intermediate age (2000–3000 years old). In younger communities, both the lack of propagules and ongoing soil formation may limit the number of species (Pärtel & Zobel 1999). In older areas, the dominance of different land use types (e.g. forests or arable fields) on mature soils may isolate grassland stands and hinder dispersal. Community species pool size also decreased with soil N content and this may be caused by processes such as interspecific competition, dispersal limitation or evolutionary constraints.

Historical human impact has probably been the most substantial on the dispersal of plants: diaspores may have been unintentionally transported together with animals and hay. Though alvars in NW Russia, Izhora plateau are geographically isolated from other alvar communities, they are floristically similar to alvars in northern Estonia (**III**, Fig. 2, 3). The historical connection between NW Russia and Estonia has been strong due to the location of Estonian and Finnish settlements on the Izhora plateau (Isachenko 1998). The trade of domestic animals during the past centuries has most likely promoted diaspore dispersal from Estonia to Izhora. Tens of thousands of domestic animals were shepherded from Estonia to the market in St. Petersburg (Moora 1964). The Izhora alvars lie exactly on this route and animals acted as dispersal vectors. Similar long-distance grassland plant dispersal by domestic animals has been described in Scandinavia (Bruun & Fritzbøger 2002; Eriksson *et al.* 2002) and in Germany (Poschlod *et al.* 1998).

Current human population density had unimodal relationship with small-scale species richness (**II**, Fig. 4). As I have shown previously, there is an extinction debt in our semi-natural communities. Due to extinction debt, the current species diversity in community level may not yet have responded to changes in human distribution densities, but the small-scale species richness reacts faster to changes in habitat quality (Pärtel & Zobel 1995). It appeared that the intermediate values of current human population densities are most beneficial for maintaining high species diversity and this demonstrates the importance of proper habitat management. In contrast to past land use and human impact, the high density of current human settlements do not support plant diversity because of increasing habitat destruction caused by urbanization and intensive agriculture (Stoate *et al.* 2001; Pautasso 2007). On the other hand, the tremendous decrease in human population density in rural areas has led to a reduction in land-use intensity (Eriksson *et al*. 2002; Poschlod & WallisDeVries 2002). This reduction results in extensive overgrowth of former semi-natural grasslands by shrubs and trees, accompanied by a decrease in species diversity (Mitlacher *et al*. 2002). Due to the lack of management, woody species invade semi-natural grasslands causing habitat degradation (Pärtel *et al.* 2005). I showed that grassland overgrowth is related to changes in soil resource heterogeneity, inasmuch as soil resource heterogeneity was much greater in forests than in grasslands (**IV**, Fig. 1; see also Pärtel *et al.* 2007). In open semi-natural grasslands, fine grass roots form a dense network and moisture and nutrients are distributed homogeneously in soil. Under such conditions, herbaceous species can compete successfully against young woody species, whereas woody species with large root systems have a competitive advantage in heterogeneous soils (Campbell *et al.*1991; Grime 1994). Single locations with deeper soil supported the invasion of woody species. Soil heterogeneity can simultaneously be a cause and an outcome of woody species invasion, as tree seedlings germinate better in heterogeneous soil, but trees themselves make soils more heterogeneous during their growth by using soil resources patchily. High soil resource heterogeneity will further enhance woody species invasion. Based on my results, I hypothesize that management keeps grassland soils more homogeneous, which may prevent the initial establishment of tree seedlings.

# CONCLUSIONS

I found that current species richness of fragmented alvar grasslands was unrelated to the current areas and connectivities of the habitat patches, but was related significantly to their past areas and connectivities, that is, to the state of the landscape prior to drastic habitat loss and fragmentation. Species richness depends ultimately on area and connectivity, leading to predicted future extinctions. This result also indicates that we need to be careful when measuring current species richness in the field, as it does not necessarily provide accurate information on current conditions of populations or communities.

Formation of currently observed species richness in communities date back centuries. I demonstrated that species richness is positively correlated to human settlement density as far back as 1000 years ago. Therefore, human land-use legacy is an important aspect in plant ecology that may contribute substantially to the current variation in biodiversity.

Historical diaspore dispersal between even remote sites has homogenized the species composition in patches of similar habitat. The isolated alvar communities in NW Russia, Izhora plateau have comparable species composition to northern Estonian alvars, probably due to intensive migration of cattle and sheep from Estonia. The traditional dispersal vectors no longer exist and the threat of species loss is increasing in these isolated communities of Izhora plateau.

During the past 70 years, alvar grasslands have lost most of their area whether due to lack of management or due to habitat destruction. Lack of management leads to invasion by woody species. In addition to the direct negative effect on biodiversity of open grasslands, trees and shrubs also change environmental conditions in ecosystems. There are striking differences in soil resource patterns between temperate semi-natural grasslands before and after woody species invasion. Soils of overgrown parts are more heterogeneous and it is possible that homogeneous soils in open grassland may prevent the initial establishment of tree seedlings. Grasslands that have been more vulnerable to overgrowth have some significantly deeper places in soil and this may favour the tree establishment.

In summary, the current species number in semi-natural highly fragmented communities may not be in an equilibrium state, as my results strongly support the concept of remnant grassland plant communities. Our current species richness reflects historical landscape structure as well as the historical density of human settlements, but future extinctions are inevitable. It is clear that proper conservation measures are urgently needed to minimize the number of future extinctions.

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# SUMMARY IN ESTONIAN

## AJALOOLISE INIMASUSTUSE JA MAASTIKUSTRUKTUURI MÕJU LOONIITUDE LIIGIRIKKUSELE

Poolloodusl ikud kooslused on ühed liigirikkaimad taimekooslused kogu Euroopas. Eesti puisniidud ja loopealsed paistavad kõrge biodiversiteedi poolest silma ka kogu maailma rohumaade seas. Samas võib vaatamata üldiselt kõrgele väärtusele soontaimede liigirikkus varieeruda nii väikeses skaalas kui ka koosluse ja regiooni tasemel, mistõttu isegi homogeensete keskkonnatingimustega kooslusetüübi piires võib rohurinde struktuur ja liigiline mitmekesisus olla väga erinev. Minu doktoritöö ülesandeks oli selgitada, miks liigirikkus Eesti looniitudel varieerub ning kuidas toimub majandamise lakkamisel niidu kinnikasvamine puittaimedega.

Laias laastus moodustub vaadeldava koosluse liigirikkus teistest sarnastest kooslustest levivate liikidega asustamise ja kohaliku väljasuremise tasakaaluna. Kooslusesse potentsiaalselt jõudvate liikide maksimaalse hulga määrab regionaalse liigifondi suurus, mis omakorda on paika pandud suureskaalaliste protsesside poolt nagu evolutsioon ja ajaloolised liikide levikumustrid. Liikide tegelik jõudmine kooslusesse sõltub aga mitmetest lokaalsematest ajaloolistest teguritest nagu sarnaste koosluste olemasolust ümbruskonnas (sidususest) ja liikide levimisvõimest. Liikide püsimine koosluses sõltub kasvukoha kvaliteedist, suurusest ja populatsioonide elujõulisusest. Poollooduslike koosluste puhul on need parameetrid omakorda seotud majandamise järjepidevusega.

Traditsiooniliste majandamisviiside lakkamise tõttu on poollooduslike rohumaade pindala eelmise sajandi keskpaigast alates aina vähenenud. Elupaikade kadumine ja nende pindala kahanemine on tänapäeval peamiseks liikide väljasuremise põhjuseks: mida väiksem on koosluselaik, seda pisemad on lokaalpopulatsioonid ja tõenäolisem, et liik mingilt alalt kaob. Peale pindala vähenemise ohustab liigirikkust ka elupaikade liigne killustumine. Mõõduka killustumise korral moodustub üht tüüpi koosluselaikudest maastikus tihe võrgustik ning liigi kadumisel koosluselaigult saabub lähedalolevatelt sarnastelt aladelt peatselt sama liik endisesse kasvukohta. Liigne killustatus viib aga koosluselaigud üksteisest liiga kaugele ning liikide ühelt alalt teisele levimine muutub aina vähem tõenäoliseks. Hästi toimiv koosluselaikude vaheline liikide levi (ehk metakooslus) on olnud oluliseks teguriks meie poollooduslike ökosüsteemide liigirikkuse kujunemisel: aastasadade vältel on soontaimeliigid püüdnud leida endale sobivaid kasvukohti ja levinud uutele, veel selle liigiga asustamata koosluselaikudele, muutes nõnda viimaseid aina rikkamaks.

Jälgisime elupaigaspetsiifiliste taimeliikide esinemist Eesti killustunud looniitudel. Looniidud on lubjarikkal aluskivimil paiknevad kuivad rohumaad, mida iseloomustab väga kõrge liigirikkus. Eesti loopealsed on sajandite vältel olnud suhteliselt stabiilse levikuga, kuid viimase 70 aasta jooksul on hävinud

70% nende pindalast. Vastavalt pindala (ning sidususe) ja liigirikkuse vahelistele seostele võib eeldada, et ka liigirikkus on neil vähenenud. Samas võib liik metakoosluselise dünaamikaga aladelt kaduda teatud hilinemisega. Populatsioonide aeglase dünaamika tõttu ei pruugi liigirikkus koheselt pärast killustumist jõuda uude tasakaaluolekusse, mis vastaks uuele maastikustruktuurile ja tekib nn. väljasuremisvõlg. Väljasuremisvõla moodustavad koosluses need liigid, kes suudavad killustumise järel lühemat või pikemat aega eluvõimelisena püsida (kuigi juba vähenenud ohtrusega). Samas ei ole elupaik neile enam kuigivõrd sobilik ja väljasuremine on vaid aja küsimus.

Tahtsin teada, kas meie loopealsetel on liigirikkus juba langenud tänapäevasele maastikustruktuurile vastava väärtuseni või on neil väljasuremisvõlg ja looalade liigirikkus vastab veel killustumisele eelnenud maastikustruktuurile. Selleks uurisin, kas loopealsete liigirikkus on seotud loolaikude ajaloolise või praeguse pindala ning sidususega (kaugusega teistest sarnastest aladest). Selgus, et loopealsete tänane liigirikkus sõltub ala ajaloolisest pindalast ja sidususest, mitte aga praegusest pindalast ja sidususest (**I**, Joon. 2). See tähendab, et endised suured liigirikkad loopealsed on ka tänapäeval jäänukitena liigirikkamad ja meie alvarite liigilisel mitmekesisusel on väljasuremisvõlg. Eeldades, et aladel, mis ei ole oma pindalast olulisel määral kaotanud, on liigirikkus jäänud võrdlemisi sarnaseks endisaegsega, hindasime väljasuremisvõla suuruseks ülejäänud looaladel umbes 40%, mis vastab ligikaudu 20 soontaimeliigile ühel looniidul. Kuna nii suurt liikide väljasuremist on oodata igal suure pindalakaoga ja killustunud loopealsel, on tulevik üpris tume. Arvestades praegust maastikustruktuuri ja liikide levikuareaale, võivad paljud neist liikidest kaduda kogu regioonist, kuigi see protsess on ilmselt veelgi aeganõudvam kui liigi kadumine üksikult loopealselt.

Saadud tulemus näitab, et tänane liigirikkus peegeldab ala ajalugu. Proovisime leida, kui kauge aja taha liigirikkuse kujunemine võib jääda. Loopealsed on tekkinud inimese tegevuse tagajärjel – juba aastatuhandete eest alustati metsa mahavõtmist, karjatamist ja niitmist. Püsiv majandamine ja metakoosluse siseselt seemnete levile kaasaaitamine on poollooduslike koosluste liigirikkuse kujunemisel väga olulisteks teguriteks. Karjakasvatuse esimesed märgid Eesti aladelt pärinevad juba 6000 aasta tagusest ajast ning tuginedes õietolmuandmetele toimus 3000 aastat tagasi märgatav tõus rohttaimede liigirikkuses. Kuna Eesti loopealsete tänane liigirikkus on seotud ajaloolise maastikustruktuuriga, on tõenäoline, et me suudame veel praegugi, vaatamata hiljutisele killustumisele, tuvastada aastasadade tagust inimmõju. Püstitasime hüpoteesi, et praegune liikide arv loopealsetel sõltub inimasustuse tihedusest hilisel rauaajal (umbes 1000 aastat tagasi). Liigirikkad alvarid said kujuneda vaid seal, kus oli piisavalt elanikke, et tekiks ulatuslik karjamaade võrgustik ja kus seeläbi toimuks loopealsetele iseloomulike liikide levi. Meie tulemused näitasidki, et tänapäeval on kõige liigirikkamad loopealsed piirkondades, kus rauaajal oli inimeste asustustihedus kõige suurem (**II**, Joon. 3). See kinnitab, et loopealsete praegune liigirikkus on vähemalt 1000-aastase ajalooga!

Ajalooliselt on soontaimede levikule kaasa aidanud ka kariloomad: loopealsetel (nagu puis- ja rannaniitudelgi) kasvab rohkesti taimi, mille seemned on justkui loodud „reisima" lamba kasukasse takerdunult. Tihti liikusid kariloomad ulatuslikul maa-alal, eriti pikad vahemaad läbiti neid ühelt alalt teisele või müügile viies. Uurisime, kas loode-Venemaal Isuri platool leiduval Ordoviitsiumi lubjakiviladestul levivate rohumaade liigiline koosseis võib olla kujunenud ajaloolise loomade transpordi tulemusena. Loopealsed levivad Ordoviitsiumi või Siluri lubjakivi avamusavadel ja looalade levik maailmas on väga piiratud. Peale Läänemere suurte saarte (Saaremaa, Muhu, Hiiumaa, Öland ja Gotland) leidub loodusid väikeste aladena lõuna-Rootsis Västergötlandis, ning mandri-Eesti lääne- ja põhjaosas. Isuri platoo taimekooslused olid siiani botaaniliselt klassifitseerimata. Leidsime, et lähimatest loopealsetest 150 km kaugusel asuvad Isuri platoo taimekooslused on tõesti loopealsed (**III**, Joon. 2), olles floristiliselt sarnased põhja-Eesti alvaritega (**III**, Joon. 3). Kuna kirjeldatud aladel ümbruskonnas sarnased kooslused puuduvad, on looliigid sinna jõudnud tõenäoliselt kariloomade abil Eesti aladelt. 1703. aastal rajas Peeter I Peterburi linna. Igal aastal värvati 20 000 inimest ehitustöödele ja kõik töötajad vajasid süüa ja riideid. Ka linna elanikkond kasvas jõudsalt: kümnekonna aastaga tõusis elanike arv 40 000 inimeseni. Peterburi turg muutus piirkonna olulisimaks kaubandussõlmeks. Eestist transporditi kariloomi Peterburi turule ja on väga tõenäoline, et siinsetelt alvaritelt pärit seemned leidsid sel kombel tee ka Isuri platoole. Ajalooliselt olid selles Venemaa piirkonnas suured eesti külad üsna elujõulise eestlaste asurkonnaga. Võimalik, et ka Ingerimaa eestlaste läbikäimine oma sugulastega Põhja-Eestis võis kaasa aidata liikide levikule.

Loopealsed on tänapäeval majandamise lakkamise tõttu jõudsalt kinni kasvamas. Paljud kunagised looalad on kattunud puude ja põõsastega. Samas leidub alasid, mis püsivad hoolimata majandamise lakkamisest veel avatuna. Uurisime, miks on mõned alvarid puude invasioonile vastuvõtlikumad kui teised ja vaatlesime erinevusi avatud ja kinnikasvanud looalade maa-alustes tingimustes. Mulla laigulisus (varieeruvus keskkonnaparameetrites) võib olla mitmete ökoloogiliste nähtuste põhjuseks kuna mõned eluvormid tunnevad end laigulisel mullal paremini kui teised. Põhja-Ameerikas tehtud töödes on leitud, et puittaimed on laigulisemas mullas soodustatumas olukorras kui rohttaimed, kuna puude idanemine on sel juhul edukam. Hiljem suudavad puud oma jämedakoelise juurestiku abil hõlmata palju suuremat ruumala ja liikuda ka üle toitainevaeste alade. Lisaks on teada, et majandamine hoiab poollooduslike koosluste mulla homogeense. Kogusime mulla- ja juureproove Eesti looniitude avatud ja kinnikasvanud osadelt. Leidsime, et puude idanemine avatud niidul on tõenäolisem, kui alal leidub üksikuid sügavama mullaga kohti. Eduka idanemise järgselt muudavad puud oma elutegevuse tulemusena mulla veelgi laigulisemaks ja soodustavad sellega edasist puittaimede pealetungi (**IV**, Joon. 1). Seega tuleb poollooduslike niitude kaitsel arvestada ka maa-aluseid ökoloogilisi protsesse.

# Kokkuvõtteks

Looalade liigirikkusel on pikk „mälu“, mis ulatub vähemalt 1000 aasta tagusesse aega. Aastasadu püsivalt majandatud poollooduslikud kooslused kaotasid eelmise sajandi teisel poolel enamuse oma pindalast. Tugevalt killustunud lookoosluste praegune liigirikkus peegeldab nende kunagist laia levikut, kuid mitte nende tänast vähenenud pindala, mistõttu tuleb liike loendades ja poollooduslike koosluste kaitset korraldades arvesse võtta ka hiljutistest maastikumuutustest tingitud tulevasi väljasuremisi. Vastasel korral võime liigirikkust oluliselt ülehinnata ja seeläbi koosluse ohustatuse taset alahinnata. Vähendamaks tulevaste väljasuremiste hulka, tuleb luua toimiv looalade võrgustik, kus aidatakse kaasa seemete levile alade vahel. Sellisesse võrgustikku tuleb kaasata ka näiliselt väheväärtuslikumad looalad, mis on aga liikidele olulisteks peatuspaikadeks. Järjepidev majandamine kõigil säilinud looaladel koos seemnete levile kaasaaitamisega takistab puude-põõsaste sissetungi ning loodetavasti vähendab ka ohtu alvarite liigirikkusele.

# TÄNUSÕNAD
## Acknowledgements

Minu kõige südamlikum tänu kuulub juhendaja Meelis Pärtelile, kelle targad nõuanded, lahke meel ja hea teaduslik vaist on mind läbi aastate saatnud. Tänan kõiki kaasautoreid: Ilkka Hanski, Jaan Liira, Martin Zobel, Triin Reitalu, Sergey Znamenzkiy. Olen tänulik kõigile, kelle välitöödelt kogutud andmeid mul oli võimalik kasutada. Välitöödel abistamise eest suur aitäh Nele Ingerpuule, Inga Hiiesalule, Inga Jüriadole ja Priit Kupperile. Välitööde kõige-kõige olulisem abiline on aga olnud Tiiu Kupper, kelleta oleks vist küll suurem osa andmeid kogumata. Aitäh Sulle Tiiu! Tänan ka Robert Szava-Kovats'it keelelise korrektuuri eest.

Ma olen väga õnnelik meie Lai 36-s pesitsevate kraadiõppurite seas valitseva vaimuerksa meelelaadi üle, tänu millele on õpingud siin instituudis olnud nii põnevad. Mul on hea meel, et ma olen siin nii toredate inimestega kohtunud ja ma loodan, et meie sõprus ja koostöö kestavad veel aastakümneid. Pille Urbast tahaksin tänada eraldi inspireeriva töökeskkonna loomise eest!

Elu on viinud mind kokku suurepärase elukaaslasega ja andnud mulle toredaimad lapsed. Aitäh teile toetuse eest Mart, Eke-Tõnis ja Luule-Mari! Soojad tänusõnad minu emale ja isale. Teile peaks tegelikult kuuluma kõik maailma ilusaimad sõnad, sest te olete parimad vanemad, kes inimesel olla saavad.

This work has been supported by Estonian Science Foundation, Swedish Institute, Finnish-Karelian research programme, EU 6FP projects ALARM and COCONUT.

# PUBLICATIONS

# CURRICULUM VITAE

## I. General

| | |
|---|---|
| **Name:** | AVELIINA HELM |
| **Date and place of birth:** | 21.03.1979, Tartu |
| **Citizenship:** | Estonian |
| **Address:** | Institute of Botany and Ecology, Lai 40, 51005 Tartu<br>+3727376263, *aveliina.helm@ut.ee* |
| **Current position:** | University of Tartu, Institute of Botany and Ecology, *Ph.D.* student |

**Education:**

| | |
|---|---|
| 2003 | University of Tartu, *M.Sc* in plant ecology and ecophysiology. Master thesis: *Spatial and temporal dynamics of species richness of Saaremaa and Muhu alvars* |
| 2001 | University of Tartu, *B.Sc* in biology |
| 1986–1997 | Tartu Karlova Gymnasium (VII Tartu Secondary School) |

**Languages spoken:** Estonian, English

**Professional employment**

| | |
|---|---|
| 2003–2007 | Institute of Botany and Ecology, University of Tartu, *Ph.D* student |
| since 2000 | Institute of Botany and Ecology, University of Tartu, temporary technical assistant |
| 1996–2000 | Estonian Literary Museum, research assistant |

## II. Scientific and research activity

**Research interests:**

Formation and persistence of species diversity in plant communities. Species diversity and genetic diversity in fragmented landscapes. Management history of semi-natural communities. Effects of underground conditions on belowground performance of plant communities.

**Publications:**

**1.1. Articles indexed by ISI Web of Science**

Pärtel, M., Helm, A., Reitalu, T., Liira, J. & Zobel, M. (2007) Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology,* 95, 574–582.

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Pärtel, M., Helm, A., Ingerpuu, N., Reier, Ü. & Tuvi, E.-L. (2004) Conservation of Northern European plant diversity: the correspondence with soil pH. *Biological Conservation,* 120, 525–531.

### 1.2. Peer-reviewed articles in other international research journals

Dengler, J., Rūsina, S., Boch, S., Bruun, H.H., Diekmann, M., Dierßen, K., Dolnik, C., Dupré, C., Golub, V.B., Grytnes, J.-A., Helm, A., Ingerpuu, N., Löbel, S., Pärtel, M., Rašomavičius, V., Tyler, G., Znamenskiy, S.R., Zobel, M. (2006) Working group on dry grasslands in the Nordic and Baltic region – Outline of the project and first results for the class Festuco-Brometea. *Annali di Botanica Nuova Serie,* 6, 1–28.

### 1.3. Popular science articles

Helm, A. & Pärtel, M. (2007) Loopealsed ajale võlgu. *Eesti Loodus,* 58, 132–135. /in Estonian/

Helm, A. (2005) Tõsi tõuseb, vale vajub. Pettusest ja sohist teaduses. In: Öpik, M., Tulva, I. & Puura, I. (eds.) Vale teooria – *Schola Biotheoretica,* 30, 121–128. /in Estonian/

Helm, A. (2002) Saaremaa loopealsete võrgustik. In: Puura, I. & Teder, T. (eds.) Võrkude teooria – *Schola Biotheoretica,* 27, 56–60. /in Estonian/

Helm, A. & Pärtel, M. (2002) Ingerimaa loopealsetel. *Eesti Loodus,* 53, 108–111. /in Estonian/

### Grants and scholarships:

Senior personnel in two grants:

ETF6619 (Tiit Teder), Diversity and dynamics of insect communities in fragmented habitats.

ETF6614 (Meelis Pärtel), Macroecological processes determining plant community diversity and function

Awarded by the Estonian Ministry Education and Research in Estonian National Contest for Young Scientists at university level:

III prize for study *Slow response of plant species richness to habitat loss and fragmentation* in 2005

Diploma for master thesis *Spatial and temporal dynamics of species richness of Saaremaa and Muhu alvars* in 2003

II prize for final paper *Species diversity and species traits: comparison of alvar vegetation of Estonia and Sweden* in 2001

**Other scientific activities**
Membership in societies:
Estonian Naturalists Society
Estonian Seminatural Community Conservation Association

Conference thesis:

Helm, A., Pärtel, M., Reitalu, T., Liira, J. & Zobel, M. (2007) Grassland diversity related to the human population density a thousand years ago. In: van Essen, R. A. (ed.) *49th Annual Conference of the International Association for Vegetation Science. New Zealand: New Home; new habitat! new ideas? Book of Abstracts*, p. 90. Palmerston North, New Zealand, 12–16 February 2007.

Helm, A., Hanski, I. & Pärtel, M. (2005) Delayed response in plant species richness to habitat loss and fragmentation. In: Erdem, Ü., Nurlu, R. M (eds.) *X European Ecological Congress Abstracts Book*, p. 289. European Ecological Federation, Turkish Ecological Society, Ege University Center for Environmental Studies. Kusadasi, Turkey, 08–13 November 2005.

# ELULOOKIRJELDUS

## I. Üldandmed

**Ees- ja perekonnanimi:** AVELIINA HELM
**Sünniaeg ja koht:** 21. märts 1979, Tartu
**Kodakondsus:** Eesti
**Aadress:** Botaanika ja ökoloogia instituut, Lai 40, 51005 Tartu
+3727376263, *aveliina.helm@ut.ee*
**Praegune töökoht, amet:** Tartu Ülikool, botaanika ja ökoloogia instituut, doktorant

**Haridus:**
2003 Tartu Ülikool, magistrikraad taimeökoloogias ja ökofüsioloogias. Magistritöö: *Saaremaa ja Muhu lookoosluste ajalis-ruumiline dünaamika*
1997–2001 Tartu Ülikool, bioloogia
1986–1997 Tartu Karlova Gümnaasium (Tartu 7. Keskkool)

**Keelteoskus:** eesti, inglise

**Töökogemus:**
2003–2007 Tartu Ülikool, botaanika ja ökoloogia instituut, doktorant
alates 2000 Tartu Ülikool, botaanika ja ökoloogia instituut, preparaator
1996–2000 Eesti Kirjandusmuuseum, assistent

## II. Teaduslik ja arendustegevus

**Peamised uurimisvaldkonnad:**
Liigirikkuse kujunemine ja püsimine taimekooslustes. Koosluste killustumine ja selle mõju liigirikkusele ja liigilisele koosseisule. Geneetiline mitmekesisus killustunud maastikes. Poollooduslike koosluste majandamise ajalugu ja selle mõju mitmekesisusele.

**Publikatsioonide loetelu:**

**1.1. Artiklid, mis on kajastatud ISI Web of Science andmebaasis**

Pärtel, M., Helm, A., Reitalu, T., Liira, J. & Zobel, M. (2007) Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology,* 95, 574–582.

Pärtel, M. & Helm, A. (2007) Invasion of woody species into temperate grasslands: Relationship with abiotic and biotic soil resource heterogeneity. *Journal of Vegetation Science,* 18, 63–70.

Helm, A., Hanski, I. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters,* 9, 72–77.

Znamenskiy, S., Helm, A. & Pärtel, M. (2006) Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. *Biodiversity and Conservation,* 15, 1797–1809.

Pärtel, M., Helm, A., Ingerpuu, N., Reier, Ü. & Tuvi, E.-L. (2004) Conservation of Northern European plant diversity: the correspondence with soil pH. *Biological Conservation,* 120, 525–531.

### 1.2. Artiklid teistes rahvusvahelistes ajakirjades

Dengler, J., Rusina, S., Boch, S., Bruun, H.H., Diekmann, M., Dierßen, K., Dolnik, C., Dupré, C., Golub, V.B., Grytnes, J.-A., Helm, A., Ingerpuu, N., Löbel, S., Pärtel, M., Rašomavicius, V., Tyler, G., Znamenskiy, S.R. & Zobel, M. (2006) Working group on dry grasslands in the Nordic and Baltic region – Outline of the project and first results for the class Festuco-Brometea. *Annali di Botanica Nuova Serie,* 6, 73–100.

### 6.3. Populaarteaduslikud artiklid

Helm, A. & Pärtel, M. (2007) Loopealsed ajale võlgu. *Eesti Loodus,* 58, 132–135.

Helm, A. (2005) Tõsi tõuseb, vale vajub. Pettusest ja sohist teaduses. Öpik, M., Tulva, I. & Puura, I. (toim.) Vale teooria – *Schola Biotheoretica,* 30, 121–128.

Helm, A. (2002) Saaremaa loopealsete võrgustik. Puura, I. & Teder, T. (toim.) Võrkude teooria – *Schola Biotheoretica,* 27, 56–60.

Helm, A. & Pärtel, M. (2002) Ingerimaa loopealsetel. *Eesti Loodus,* 53, 108–111.

### Saadud uurimistoetused ja stipendiumid:

Põhitäitja kahes grandis:

GBGBO6619 (Tiit Teder), Liigilise mitmekesisuse mustrid ja dünaamika putukatel fragmenteeritud elupaikades.

GBGBO6614 (Meelis Pärtel), Makroökoloogilised protsessid taimekoosluse mitmekesisuse ja talitluse määratlejatena.

Eesti Haridus- ja Teadusministeerium on määranud Üliõpilaste teadustööde riikliku konkursi raames:

III preemia uurimuse "*Slow response of plant species richness to habitat loss and fragmentation*" eest aastal 2005

Diplom magistritöö "Saaremaa ja Muhu lookoosluste ajalis-ruumiline dünaamika" eest aastal 2003

II preemia lõputöö "Liigiline mitmekesisus ja liikide tunnused: Eesti ja Rootsi loopealsete taimkatte võrdlus" eest aastal 2001

**Muu erialane tegevus**
Osavõtt erialastest organisatsioonidest:
Eesti Looduseuurijate Selts
Pärandkoosluste Kaitse Ühing

Konverentside ettekanded:

Helm, A., Pärtel, M., Reitalu, T., Liira, J. & Zobel, M. (2007) Grassland diversity related to the human population density a thousand years ago. In: van Essen, R. A. (ed.) *49th Annual Conference of the International Association for Vegetation Science. New Zealand: New Home; new habitat! new ideas? Book of Abstracts*, p. 90. Palmerston North, New Zealand, 12–16 February 2007.

Helm, A., Hanski, I. & Pärtel, M. (2005) Delayed response in plant species richness to habitat loss and fragmentation. In: Erdem, Ü., Nurlu, R. M (eds.) *X European Ecological Congress Abstracts Book*, p. 289. European Ecological Federation, Turkish Ecological Society, Ege University Center for Environmental Studies. Kusadasi, Turkey, 08–13 November 2005.

# DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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