Low shrub cover in alvar grasslands increases small-scale diversity by promoting the occurrence of generalist species

Leichte Verbuschung von Alvar-Kalkmagerrasen hat einen positiven Effekt auf die Artenvielfalt durch die Förderung generalistischer Arten

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Abstract

Dry calcareous grasslands in Europe are renowned for their high plant diversity. However, declining habitat areas and highly fragmented distribution threaten the long-term persistence of this valuable habitat type. In Estonia the decline of traditional grassland management and subsequent encroachment of shrubs has resulted in a substantial loss of alvar grasslands – a particularly rare and species-rich type of calcareous grassland. It is known that a shrub cover of more than 70% decreases the alvar grassland species richness. At the same time, a shrub cover of 30% is considered optimal for alvar grasslands and thus a target state for habitat restoration. However, very little is known about the effect of low shrub cover on environmental conditions and species composition of alvar grasslands. Our aim was to detect to what extent the small-scale plant diversity and species composition is influenced by low shrub cover (less than 30%). We hypothesized that even a low shrub cover can have an effect on the environmental conditions of alvar grasslands.

We sampled small-scale plant species richness, shrub cover and abiotic environmental conditions such as light, soil moisture, soil pH and soil depth in 10 metre long transects ($n = 33$) subdivided into 10 cm × 10 cm plots in Estonian alvar grasslands. Structural equation modelling was used to quantify the direct and indirect effects of shrub cover on the richness of characteristic alvar species and on the richness of generalist species.

We found that low shrub cover of up to 30% increased total and generalist species richness directly and indirectly by increasing the light heterogeneity. Alvar characteristic species richness was not related to low shrub cover values. This suggests that when estimating the effects of shrub cover on species richness and on conservation needs of grasslands, habitat specificity of species needs to be taken into account.

Keywords: alvar grassland, grassland conservation, species richness, structural equation modelling, woody plants

Erweiterte deutsche Zusammenfassung am Ende des Textes

1. Introduction

Temperate, oligo- to mesotrophic, semi-natural grasslands have the highest small-scale plant species richness in the world (WILSON et al. 2012), yet these habitat types are globally endangered (CEBALLOS et al. 2010). In Europe most of the historically developed semi-natural grasslands have either been abandoned or the traditional extensive grassland management has been replaced by intensive agricultural practices during the past century (ROSENTHAL et al. 2012, STRIJKER 2005). Both types of land use change resulted in shrub encroachment in grasslands and in changed environmental parameters and species composition (AAVIK et al. 2008, PETŘÍK et al. 2011, PIHLGREN & LENNARTSSON 2008, PÄRTEL & HELM 2007, PÄRTEL et al. 1999a), ultimately leading to large decreases in grassland habitat area (POSCHLOD et al. 2005). Shrub encroachment in grassland is often followed by a decline in characteristic grassland species richness (GRIME 2002, LIMB et al. 2010, PÄRTEL & HELM 2007, ÖCKINGER et al. 2006). At the same time, shrub encroachment can facilitate the establishment of species that are better adapted to these new conditions, e.g. generalist species or species from other habitat types (KIVINIEMI & ERIKSSON 2002). The mechanisms by which shrub cover influences grassland species composition includes a reduction in light availability (LIMB et al. 2010), a shift in soil nutrient and water availability (HUXMAN et al. 2005, MIWA & REUTER 2010), and a decrease in soil pH (JOBBAGY & JACKSON 2003).

Environmental changes related with shrub encroachment not only modify the quantity and quality of different parameters, but also their spatial heterogeneity (PÄRTEL & HELM 2007). Spatial environmental heterogeneity is caused by a patchy distribution of resources in space (WIENS 2000). PÄRTEL & HELM (2007) found that small-scale environmental factors such as soil moisture and nutrient content varied notably more in forests than in grasslands. This is because the extensive root systems of woody plants use resources patchily, and relatively homogeneous grassland environments will become more heterogeneous after shrub encroachment (BEKELE & HUDNALL 2006, LIU et al. 2011, PÄRTEL & HELM 2007). Habitat heterogeneity can also have influence on the species diversity (CLARK et al. 1998). At larger scales the influence of environmental heterogeneity on plant diversity is usually presumed to be positive according to niche theory (CLARK et al. 1998, TILMAN 1982); at smaller scales, however, the influence can also be negative (LAANISTO et al. 2012, PAUSAS & AUSTIN 2001, TAMME et al. 2010).

In this study we focus on the effect of low-cover shrub encroachment on alvar grassland plant species richness and composition. Alvars are calcareous species-rich semi-natural grasslands, mostly occurring on the outcrops of Ordovician or Silurian limestone (LAASIMER 1965). Alvar grasslands are characterised by very shallow (< 20 cm) soils and a distinctive species composition consisting of calciphilous, light-demanding species (LAASIMER 1965, PAAL 1997). Distribution of alvar grasslands is very limited: they mostly occur in Sweden and Estonia, and to lesser extent a similar habitat type is also present in Canada and Russia (SCHAEFER & LARSON 1997, ZNAMENSKIY et al. 2006). For centuries alvar grasslands have been more or less continuously mown and grazed, which has kept the shrub cover low or even entirely absent (LAASIMER 1965, POSKA & SAARSE 2002; Fig. 1). In Estonia alvar grasslands are currently mostly abandoned and rapidly overgrown by pine (*Pinus sylvestris*) and juniper (*Juniperus communis*) (Fig. 2). Since the 1930s the surface area of alvars has decreased from 43,500 hectares to approx. 5000 hectares (HELM et al. 2006). Without large-scale restoration measures, their further persistence in Estonia is doubtful (HELM et al. 2006, PÄRTEL & HELM 2007).

Fig. 1. Rajametsa alvar grassland in western Estonia. One of the few well-preserved and currently continuously grazed alvar grassland (photo: A. Helm).

Abb. 1. Magerrasen des Rajametsa-Alvars in West-Estland. Es handelt sich dabei um einen der wenigen noch gut erhaltenen und derzeit noch kontinuierlich beweideten Alvare in Estland (Foto: A. Helm).

Fig. 2. Abandoned and highly overgrown (mostly by pines and junipers) Pivarootsi alvar grassland in western Estonia (photo: L. Saar).

Abb. 2. Aufgegebener und stark mit v. a. Kiefer und Wacholder verbuschter Magerrasen des Pivarootsi-Alvars in West-Estland (Foto: L. Saar).

Alvar grasslands with a shrub cover of 30% are considered to be in the best condition, and this cover is also recommended as a desirable state following habitat restoration (HELM 2011). However, although several studies have shown that a shrub cover of more than 70% rapidly decreases alvar grassland species richness (PÄRTEL et al. 1999b, REJMÁNEK & ROSÉN 1988), little is known of how a low shrub cover (up to 30%) influences the environmental conditions and species richness of alvar grasslands. The influence of woody species cover on herbaceous vegetation is most pronounced at small scales (REJMÁNEK & ROSÉN 1992). It is also important to take into account that habitat characteristic species and more widespread generalist species may be differently related to low shrub cover due to the possibly differing requirements for habitat conditions (PYKÄLÄ et al. 2005, REJMÁNEK & ROSÉN 1992).

The aim of this study is to detect the extent to which shrub encroachment affects plant species richness and composition in currently open and visually well-preserved habitat patches. We hypothesize that even a low cover of shrubs (up to 30%) influences the small-scale richness of grassland plants via altering the environmental conditions or increasing environmental heterogeneity. More specifically we test whether the richness of alvar characteristic species and generalist species are influenced differently by environmental changes triggered by low shrub cover.

2. Material and methods

A total of 33 alvar grasslands (EC Habitats Directive habitat type 6280* "Nordic alvar and precambrian calcareous flatrocks") on the Estonian islands of Saaremaa and Muhu (Fig. 3; ca. 58º N, 22–23º E) were visited during August 2010. Each grassland belonged to the "*Avenetum alvarense*" type (PÄRTEL et al. 1999a) – however, this name is illegitimate according article 34a ICPN (WEBER et al. 2000) but is given here because no legitimate name exists so far (for further details on dry grassland communities of Saaremaa see BOCH & DENGLER (2006)). The sampled grasslands represented almost all of the best-preserved alvar grasslands in Estonia. The climate on these islands is maritime with a mean temperature of 21 ºC in July (summer), -8.2 ºC in January (winter), and a mean annual precipitation of 679 mm (EMHI 2011).

To collect data describing the small-scale species richness and environmental parameters, we established a single transect of 0.1 m × 10 m in each alvar grassland. Transects were located in the open areas of grassland patches to represent the typical environmental conditions of good-quality (i.e. not overgrown) alvar grasslands. Each transect was divided into 100 plots of 10 cm × 10 cm. In each plot we recorded the vascular plants and measured soil pH, soil temperature, soil moisture, relative light availability, and soil depth in 2010. All measurements of abiotic variables were carried out during the shortest possible time span once in each grassland site in the beginning of August.

Soil pH was measured using a HI-99121 pH meter in combination with a HI-1292D electrode (Hanna Instruments, Padova, Italy). Soil temperature and moisture were measured with a Delta-T WET-2 sensor (Delta-T Devices, Cambridge, UK). Soil pH, temperature, and moisture were measured at 10 cm below soil surface at a central point in each plot. Light availability was measured using a Li-Cor (Lincoln, Nebraska, USA) LI-250 Light Meter and LI-190SA Quantum Sensor. To minimise between-plot variation of light availability, we calculated relative light availability (below-grass light availability/above-grass light availability). Soil depth was measured using a thin metal rod in the centre and in all four corners of each plot to a maximum depth of 40 cm and subsequently averaged per plot.

To study the influence of low-cover shrub encroachment on small-scale species richness and on environmental parameters, we mapped the position and canopy cover of all shrubs around transects on gridded paper by using measuring tape. Juniper (*Juniperus communis*) and pine (*Pinus sylvestris*) were dominant woody plant species. Common buckthorn (*Rhamnus cathartica*) and alder buckthorn (*Fran-*

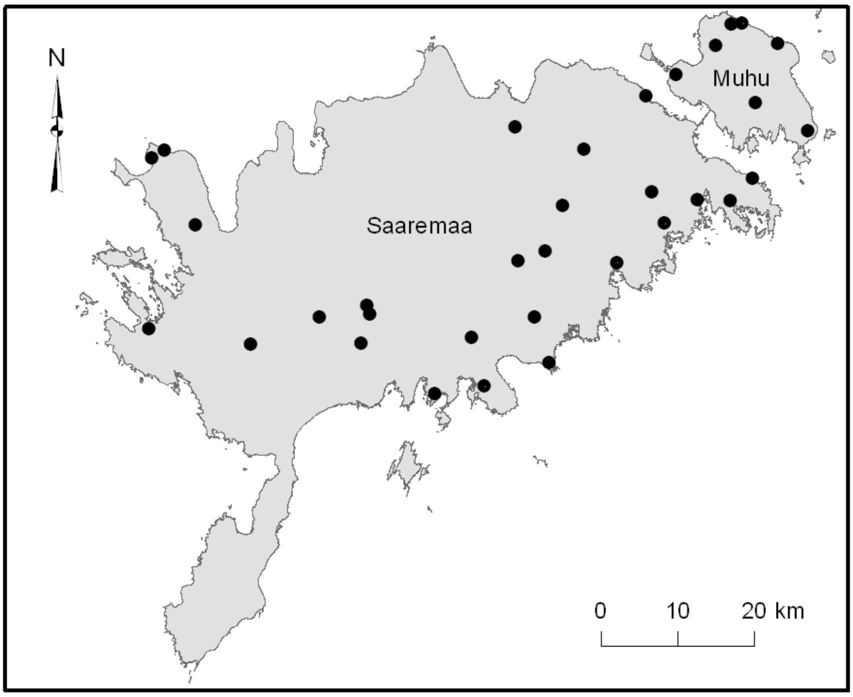

Fig. 3. Location of the studied alvar grassland patches (n = 33) on the Saaremaa and Muhu islands in Estonia.

Abb. 3. Orte der 33 untersuchten Alvar-Magerrasen auf den Inseln Saaremaa und Muhu in Estland.

gula alnus) were also present, but to a much lesser extent. After sampling we digitised the data and calculated the percentage of shrub cover around transects within one meter radius using the geographic information system ArcGIS 9.2 (ESRI 2004).

In addition to total species richness, we distinguished the characteristic and generalist species. We defined characteristic species as species that grow preferably on calcareous alvar grasslands and are rarely present in other communities. Generalist species were defined as species occurring predominantly in other habitat types. Most of the species considered generalists were widespread species inhabiting open habitat types, but also some forest and ruderal species (see Appendix 1 for species lists). To categorise species as characteristic or generalist species, we used lists of the Estonian alvar grassland classification (PÄRTEL et al. 1999a), main habitat descriptions of the Estonian Flora (KUKK 1999), characteristic species lists of Estonian semi-natural communities (PÄRTEL et al. 2007), and expert opinions (M. Pärtel, A. Helm).

For each transect we calculated the mean species richness and soil depth over 100 plots. Since the soil pH, temperature, moisture, and relative light availability depend on local weather conditions and can also vary significantly throughout the year, we used the coefficient of variation (CV, i.e. standard deviation divided by the mean) for these parameters. Coefficient of variation is a measurement of environmental heterogeneity (ETTEMA & WARDLE 2002, TAMME et al. 2010); it provides information on the relative variation of the data, which can be compared for different sites and time-periods (PÄRTEL & HELM 2007). All variables were tested for normal distribution of residuals and, if deemed necessary, log-transformed, inverted, or square root transformed.

We used structural equation modelling (SEM) (GRACE 2006) to explore and quantify the direct and indirect effects of environmental variables and shrub cover on 1) total species richness, 2) characteristic species richness and 3) generalist species richness. In a field study it is impossible to separate between direct effects and indirect effects via variables that are not measured during the study. For simplicity, we denote the shrub cover effect as ‘direct’ when the cover *per se* was significantly related to species number, not via another measured environmental factor. In a first step, we considered the influence of all measured environmental parameters, but only those showing an influence on species richness were included in the final models. Overall model fit was assessed using the chi-square statistic (χ^2), the root mean square error of approximation (RMSEA), and the comparative fit index (CFI). A model can be accepted when the P-value associated with a χ^2 and RMSEA is insignificant. A CFI-value > 0.95 indicates a good fit of the model (GRACE 2006). All statistical analyses were made using IBM SPSS Amos 19.0 (ARBUCKLE 2010).

3. Results

The shrub cover surrounding the 33 transects varied between 0 and 32% (see Appendix 1 for detailed information on all parameters). We found a total number of 113 vascular plant species: 32 grassland characteristic species and 81 generalists (see also Appendix 2). There was no significant correlation between the number of characteristic and generalist species ($r = 0.28$, $P = 0.10$). Models explained 32% of the variation in total, 18% of the variation in characteristic species richness, and 40% of the variation in generalist species richness (Fig. 4 and 5). An increase in shrub cover increased total and generalist species richness both directly and indirectly via light heterogeneity (Fig. 4 and 5B; Table 1). The richness of characteristic species depended positively on soil depth, but there was no relationship with shrub cover (Fig. 5A; Table 1). Soil pH and soil temperature were excluded from final models as they had no significant relationship with any of the other parameters. Also no relationship was found between shrub cover and soil depth in any of the models. A negative relationship was found between soil moisture heterogeneity and generalist species richness (Fig. 5B). Soil moisture heterogeneity was mainly determined by soil depth, but not by shrub cover (Fig. 4 and 5).

4. Discussion

Shrub encroachment causes much concern for dry calcareous grasslands in Estonia (PÄRTEL et al. 1999b) as it has been shown that total plant diversity starts to decline quickly once the shrubs have reached ~70% cover (REJMÁNEK & ROSÉN 1988). For this reason conservation targets are aimed at keeping the shrub cover at 30% or less (HELM 2011). We found that low shrub covers had no influence on the small-scale richness of grassland characteristic species. However, habitat generalist species richness and total species richness were positively related to increasing shrub cover. Our findings indicate that the increase of generalist species richness with increasing shrub cover should be taken into consideration when planning habitat conservation and restoration.

The structural equation models comprising shrub cover and environmental factors such as soil depth, soil moisture heterogeneity, and light heterogeneity described 40% of the variation in generalist species richness, but only 18% of the variation in characteristic species richness. This difference indicates that the local variables examined in our study have a stronger influence on the generalist species richness, whereas the characteristic species richness may depend more on large-scale processes. On the landscape scale, it has been shown previously that species richness in Estonian alvar grasslands is largely dependent on large-scale habitat configuration, historical land use, and human population density (GAZOL et al. 2012, HELM et al. 2006, PÄRTEL et al. 2007).

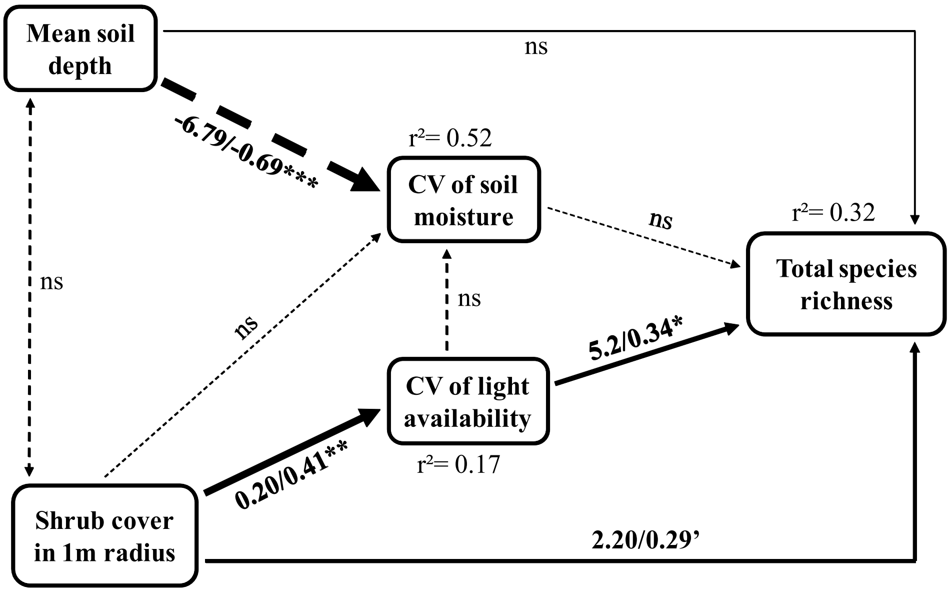

Fig. 4. Structural equation model of direct and indirect relationships between total species richness, environmental parameters, and shrub cover within a 1 m radius of the plots. Numbers on the arrows indicate unstandardised/standardised estimates of the relationships and their statistical significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$; ', $P < 0.10$; ns, non-significant. The width of the arrow is proportional to the effect of the variable. Solid lines indicate positive, dashed lines negative relationships. Double-headed arrows show unanalysed relationships, single-headed arrows direct causal relationships between parameters. Also shown are the r^2 values of the endogenous variables. Statistics of model overall fit are: CFI = 1; RMSEA = 0, $P = 0.47$; $\chi^2 = 0.54$, $P = 0.46$.

Abb. 4. Strukturgleichungsmodel der direkten und indirekten Beziehungen zwischen der Gesamtartenvielfalt, verschiedenen Umweltfaktoren und dem Grad der Verbuschung im 1-m-Radius um die Probeflächen. Die Zahlen an den Pfeilen zeigen die unstandardisierten/standardisierten Schätzwerte der Beziehungen und ihre statistische Signifikanz: *, $P < 0{,}05$; **, $P < 0{,}01$; ***, $P < 0{,}0001$; ', $P < 0{,}10$; ns, nicht signifikant. Die Pfeildicke ist proportional zur Stärke des Effekts der betreffenden Variablen. Durchgehende Linien zeigen positive Beziehungen und Punktlinien negative Beziehungen an. Pfeile mit zwei Spitzen zeigen nicht analysierte Beziehungen und Pfeile mit einer Spitze direkte kausale Beziehungen an. Ebenfalls sind die r^2-Werte der endogenen Variablen dargestellt. Die statistischen Kennwerte des Gesamtmodels lauten: CFI = 1; RMSEA = 0, $P = 0{,}47$; $\chi^2 = 0{,}54$, $P = 0{,}46$.

Shrub cover influenced the total and the generalist species richness both directly and indirectly by increasing the light heterogeneity. Trees and shrubs can have facilitative abilities by creating suitable microhabitats for germination; by changing nutrient quantity, availability, and variability; by transforming soil chemical composition, offering wind shelter, protecting from herbivores, or changing the composition of soil microorganisms (CALLAWAY 2007, FRANCO & NOBEL 1989). The indirect positive effect of shrub cover on generalist species richness via increasing the small-scale light heterogeneity can be partly explained with the classical niche theory: heterogeneous habitat conditions provide suitable habitat niches for different species (CLARK et al. 1998, RŪSIŅA et al. 2013, TILMAN 1982). Most likely, however, a decrease of full-light availability and a change in average light conditions with increasing light heterogeneity can make grasslands more suitable for species preferring shadier conditions (TAMME et al. 2010).

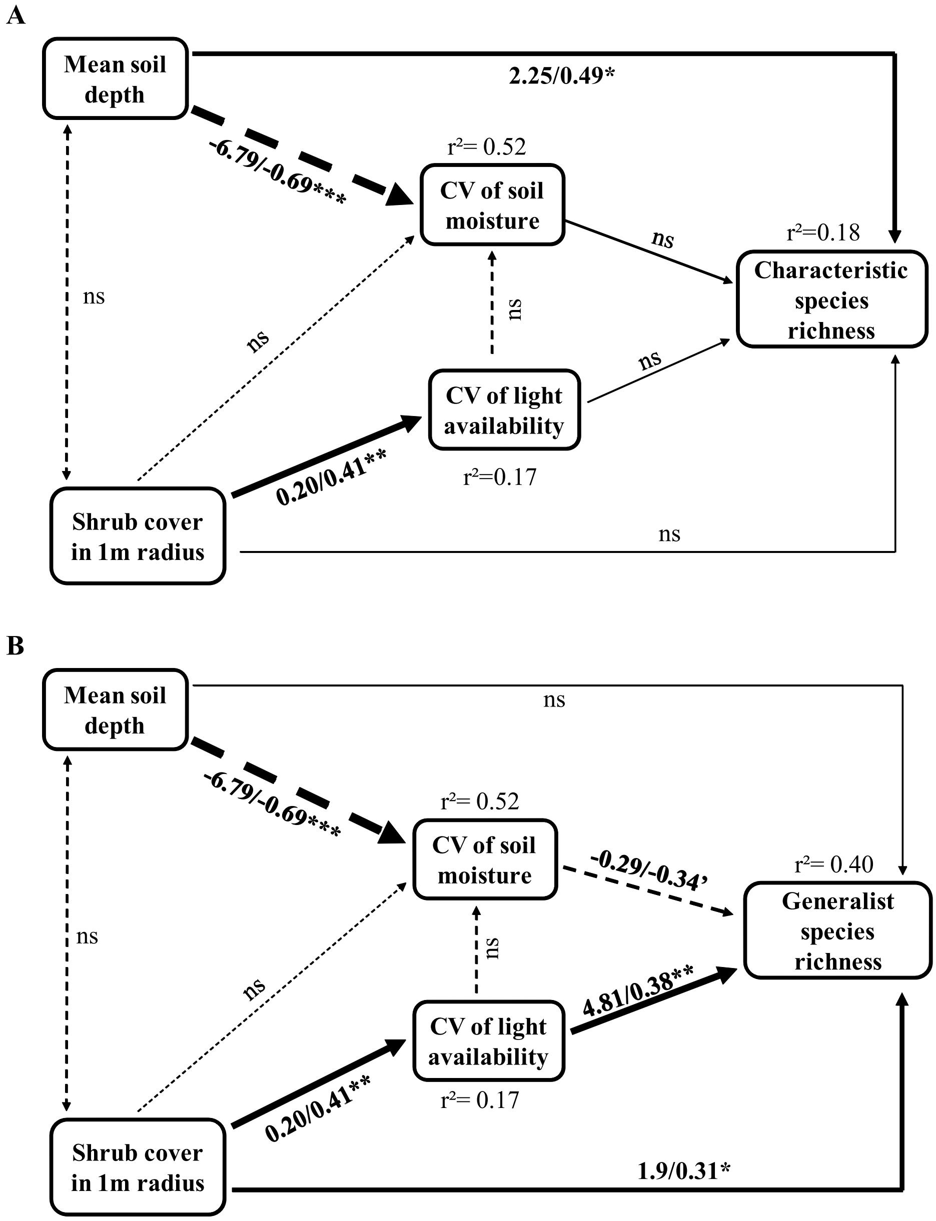

Fig. 5. Structural equation models of direct and indirect relationships between characteristic species richness (A) and generalist species richness (B), environmental parameters, and shrub cover within a 1 m radius of the plots. Numbers near the arrows indicate unstandardised/standardised estimates of the relationships and their statistical significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$; ’, $P < 0.10$; ns, non-significant. The width of the arrow is proportional to the effect of the variable. Solid lines indicate positive, dashed lines negative relationships. Double-headed arrows show unanalysed relationships, single-headed arrows direct causal relationships between parameters. Also shown are the r^2 values of the endogenous variables. Statistics of characteristic and generalist species models overall fit are: CFI = 1; RMSEA = 0, $P = 0.47$; $\chi^2 = 0.54$, $P = 0.46$.

Abb. 5. Strukturgleichungsmodel der direkten und indirekten Beziehungen zwischen Artenvielfalt der Habitatspezialisten und Habitatgeneralisten, Umweltparametern und Deckungsgrad von Sträuchern in einem 1m Radius. Die Zahlen an den Pfeilen zeigen die unstandardisierten/standardisierten Schätzungen der Beziehungen und ihre statistische Signifikanz: *, $P < 0,05$; **, $P < 0,01$; ***, $P < 0,0001$; ’, $P < 0,10$; ns, nicht signifikant. Die Breite des Pfeils ist proportional zum Effekt der Variable. Durchgehende Linien zeigen positive Beziehungen und gepunktete Linien negative Beziehungen. Zweispitzige Pfeile zeigen nicht analysierte Beziehungen und einspitzige Pfeile direkte kausale Beziehungen zwischen Parametern. r^2 endogener Variablen ist ebenfalls dargestellt. Die Parameter des Gesamtmodels sind: CFI = 1; RMSEA = 0, $P = 0,47$; $\chi^2 = 0,54$, $P = 0,46$.

We also found a negative small-scale heterogeneity-diversity relationship between generalist species richness and soil moisture heterogeneity. A negative diversity-heterogeneity relationship has been found to occur mostly only at small scales, and novel explanations such as microfragmentation theory have been presented to explain this slightly counterintuitive relationship (TAMME et al. 2010). Microfragmentation can be seen as a too fragmented occurrence of suitable environmental conditions at small scale, making the conditions unsuitable for species that require a less heterogeneous environment (LAANISTO et al. 2012, TAMME et al. 2010).

Characteristic species richness showed no direct or indirect relationship with shrub cover, contrary to our initial expectations. Many species characteristic to alvar grasslands originate from steppe and tundra regions and are adapted to open habitats with good light availability (LAASIMER 1965). Previously, REJMÁNEK & ROSÉN (1992) have found that a juniper cover exceeding 10% already decreased the number of habitat-characteristic species in Swedish alvar grasslands, whereas the total species richness increased on account of ruderal and forest species. The maximum shrub cover value in our study was 32%, and although this low cover already showed to increase the richness of generalist species, it does not yet have a negative influence on light-demanding characteristic species. Of the tested parameters, the

Table 1. Total, direct, and indirect effects of environmental parameters and shrub cover on total, characteristic, and generalist species richness according to structural equation modelling. The unstandardised and standardised effects are separated with a ‘/’. CV = coefficient of variation. The path diagrams are shown in Fig. 4 and 5.

Tabelle 1. Gesamte sowie direkte und indirekte Effekte der Umweltfaktoren und des Grads der Verbuschung auf den Gesamtartenreichtum und den Reichtum an charakteristischen und generalistischen Arten nach einem Strukturgleichungsmodel. Die unstandardisierten und standardisierten Effekte sind durch ein ‘/’ getrennt. CV = Variationskoeffizient. Die Pfaddiagramme werden in Abb. 4 und 5 gezeigt.

	Effect	CV of light availability	CV of soil moisture	Mean soil depth	Shrub cover
Total species richness	Total	5.45 / 0.36	-0.10 / -0.10	2.15 / 0.21	3.21 / 0.43
	Direct	5.25 / 0.34	-0.10 / -0.10	1.41 / 0.14	2.20 / 0.29
	Indirect	0.20 / 0.01	–	0.74 / 0.07	1.00 / 0.13
Characteristic species richness	Total	0.92 / 0.12	0.09 / 0.17	1.84 / 0.37	0.72 / 0.19
	Direct	1.09 / 0.14	0.09 / 0.17	2.45 / 0.49	0.44 / 0.12
	Indirect	-0.16 / -0.02	–	-0.61 / -0.12	0.28 / 0.07
Generalist species richness	Total	5.36 / 0.43	-0.29 / -0.34	0.70 / 0.08	2.70 / 0.44
	Direct	4.81 / 0.38	-0.29 / -0.34	-1.28 / -0.15	1.90 / 0.31
	Indirect	0.54 / 0.04	–	1.99 / 0.24	0.80 / 0.13

only factor influencing the characteristic species richness was the soil depth, which was positively related to species number. Alvar grasslands can have very shallow soils (PÄRTEL et al. 1999a), and the small-scale richness of habitat characteristic species may be hindered in extreme environmental conditions (LAASIMER 1965). Interestingly, soil depth had no influence on generalist species richness. This might be explained by the result that generalist species richness was to a large extent influenced by increasing shrub cover, which in turn was not related to soil depth.

Except for the significant effect of modifying the light conditions, shrub cover had no significant influence on other environmental factors such as soil moisture, pH, and temperature. It is likely that the shrub cover around the studied transects was too low to have a measurable effect on most of the environmental conditions. The effect of shrubs on environmental conditions might also be more pronounced during certain time periods or under certain climatic conditions, and although we used the heterogeneity instead of mean values, the snapshot sampling design has only a limited capacity to detect year-round effects. Similarly to a previous study on alvar grasslands (PÄRTEL & HELM 2007), we found no relationship between soil depth and shrub cover, indicating that grassland overgrowth is probably more related to land use and time since abandonment than to initial environmental conditions (ROSÉN 2006).

Our results indicate that even a low shrub cover has an effect on the biodiversity and the light conditions of calcareous semi-natural grasslands. However, habitat characteristic and generalist species react differently to shrub encroachment. Shrub cover values of up to 30% increase the total vascular plant species richness on account of generalist species, but do not decrease the richness of habitat characteristic species. The results of the current study indicate that a shrub cover of less than 30% can be considered suitable for persistence of habitat characteristic species in alvar grasslands. However, the increase of generalist species can decrease the quality in alvar grasslands due to the relative decline of alvar characteristic species richness. Moreover, shrub colonisation in dry grasslands is connected with a high proportion of juvenile shrubs that have not yet reached their full size. These juvenile shrubs bear the danger of fast individual growth, which will cause negative consequences for dry grasslands within short time. Also the number of diaspores which may increase rapidly during shrub development may make stable stages of shrub encroachment difficult or even impossible. Finally, shrubs produce not only habitats for mesophilous (generalistic) plant species but also safe sites for own progeny (HAUGO et al. 2013, PÄRTEL & HELM 2007), or shrubs may spread quickly by polycormons. In general, the impact of a self-dynamical shrub encroachment on grassland richness is less studied so far but must not be neglected and therefore should further be investigated.

Erweiterte deutsche Zusammenfassung

Einführung – Kalkmagerrasen zählen auf kleiner räumlicher Skala zu den weltweit artenreichsten Vegetationstypen (WILSON et al. 2012); gleichzeitig sind sie weltweit gefährdet. In Europa wurden in den letzten Jahrzehnten viele der sich über historische Zeiträume entwickelten Kalkmagerrasen entweder aufgegeben oder die traditionelle extensive Bewirtschaftungsart wurde durch eine intensive ersetzt (STRIJKER 2005). Dies hat entweder zum Totalverlust durch Verbuschung oder zu veränderten Umweltbedingungen und damit zu einer veränderten Artenzusammensetzung der Magerasen geführt (POSCHLOD et al. 2005). Mit der Verbuschung geht i.d.R. eine Abnahme des Reichtums an charakteristischen Pflanzenarten einher (ÖCKINGER et al. 2006). Gleichzeitig fördert Verbuschung diejenigen Arten, die besser an die veränderten Umweltbedingungen angepasst sind, z. B. generalistische Arten, oder solche, die normalerweise in anderen Habitaten wachsen (KIVINIEMI & ERIKSSON 2002). Die Mechanismen, mit denen eine Verbuschung die Magerrasen beeinflusst, umfasst z. B. die Abnahme des Lichtgenusses, Veränderungen im Nährstoff- und Wasserangebot sowie eine Abnahme des pH-Werts des Bodens. Solche Veränderungen in den Umweltbedingungen umfassen jedoch nicht nur qualitative und quantitative Aspekte, wie z. B. die Verfügbarkeit an Ressourcen, sondern auch die räumliche Strukturierung der Umwelt (PÄRTEL & HELM 2007). In dieser Studie untersuchen wir die Auswirkung einer leichten Verbuschung auf den Artenreichtum und die Artenzusammensetzung von Alvar-Magerrasen in Estland. Alvare sind baumloses Grasland mit einer charakteristischen Flora und Fauna auf flachgründigem (< 20 cm) felsigem Kalkuntergrund der vom Eis der Eiszeiten mehr oder weniger eben gehobelt wurde. In Estland hat der Rückgang der traditionellen Magerrasenbewirtschaftung und nachfolgenden Verbuschung zu einem erheblichen Verlust an Alvar-Magerrasen geführt. Ein Verbuschungsgrad der Alvare von mehr als 70% führt bekanntermaßen zur Abnahme des Artenreichtums, während ein Verbuschungsgrad von 30% oft als optimal betrachtet wird und z. B. bei Pflege- oder auch Wiederherstellungsmaßnahmen als Entwicklungsziel gilt. Insgesamt ist jedoch wenig Konkretes über die Auswirkung einer geringen Verbuschung auf die Umweltbedingungen und die Artenzusammensetzung der Alvar-Magerarsen bekannt.

Ziel dieser Studie ist die Einschätzung der Auswirkung einer leichten Verbuschung auf den Artenreichtum und die Artenzusammensetzung in offenen, visuell noch gut erhaltenen Alvar-Magerrasen. Wir vermuteten, dass sich bereits eine relativ geringe Verbuschung von bis zu 30% Deckung auf den kleinräumigen Pflanzenartenreichtum auswirkt indem die Verbuschung zu einer Veränderung in den Umweltbedingungen bzw. Steigerung der kleinräumigen Umweltheterogenität führt. Speziell untersuchten wir, ob Alvar-charakteristische Pflanzenarten durch veränderte Umweltbedingungen infolge leichter Verbuschung in ihrem Reichtum anders beeinflusst werden als generalistische Arten ohne Bindung an Alvare.

Methoden – Wir untersuchten insgesamt 33 Alvar-Magerrasen (FFH-Lebensraumtyp 6280* „Nordische Alvar-Trockenrasen und flache praekambrische Kalkfelsen“) auf den estnischen Inseln Saaremaa und Muhu (Abb. 1–3; ca. 58° N, 22–23° O). Diese Halbtrockenrasen werden hier als „*Avenetum alvarense*“ bezeichnet, obwohl dieser Name nach Artikel 34a ICPN (WEBER et al. 2000) ungültig ist, da kein gültiger Assoziationsname bekannt ist.

Um den Artenreichtum der Gefäßpflanzenarten auf kleiner räumlicher Skala in Abhängigkeit von den Umweltbedingungen zu beschreiben, wurde in 30 Magerasen jeweils ein Transsekt von 10 m Länge und 0,1 m Breite angelegt und in 100 10 cm × 10 cm-Probeflächen unterteilt. Im August 2010 wurden in jeder Probefläche alle Gefäßpflanzenarten aufgenommen sowie der pH-Wert, die Temperatur, Feuchte und Gründigkeit des Bodens sowie der relative Lichtgenuss der Vegetation gemessen. Um den Einfluss einer leichten Verbuschung auf den Artenreichtum und die Umweltbedingungen zu untersuchen, wurde mit Hilfe eines Maßbands die Position aller angrenzenden Gebüsche in Karopapier eingezeichnet und deren Deckung geschätzt. Anschließend wurden die Daten digitalisiert und der Deckungsgrad der Gebüsche innerhalb eines 1-Meter-Radius um die Transsekte mit Hilfe eines Geographischen Informationssystem (ArcGIS 9.2) berechnet. Wir nutzen Strukturgleichungsmodelle (SEM) um direkte und indirekte Effekte der Umweltvariablen und dem Verbuschungsgrad auf den 1) Gesamtartenreichtum sowie den Reichtum an 2) Alvar-charakteristischen und 3) generalistischen Arten zu quantifizieren.

Ergebnisse – Der Deckungsgrad der Gebüsche in der Umgebung der 33 Transsekte variierte zwischen 0% und 32% (s. Anhang 1 für detaillierte Informationen). Insgesamt fanden wir 113 Gefäßpflanzenarten, davon 32 Alvar-charakteristische Arten und 81 generalistische Arten ohne Bindung an Alvar-Magerrasen (s. Anhang 2). Leichte Verbuschung steigerte sowohl direkt als auch indirekt (durch Erhöhung der Heterogenität des Lichtgenusses) den Artenreichtum an Generalisten und damit auch den Gesamtartenreichtum (Abb. 4 und 5B, Tab. 1). Der Reichtum an Alvar-charakteristischen Pflanzenarten wurde dagegen vom Verbuschungsgrad nicht beeinflusst (Abb. 5A, Tab. 1).

Diskussion – Unsere Ergebnisse zeigen, dass eine leichte Verbuschung einen positiven Einfluss auf die Diversität an Gefäßpflanzenarten von Kalkmagerrasen hat, indem die Heterogenität des Lichtgenusses gesteigert wird. Dadurch können sich halbschattenliebende Arten ansiedeln, ohne dass die charakteristischen Arten der Magerrasen darunter leiden. So reagierten in unserer Studie lediglich die generalistischen nicht jedoch nicht die charakteristischen Arten der Magerrasen auf leichte Verbuschung. Verbuschung von bis zu 30% steigert also den Artenreichtum durch Zunahme der generalistischen Arten ohne den Artenreichtum der für Magerrasen charakteristischen Arten zu reduzieren. Eine Verbuschung von weniger als 30% könnte daher die Persistenz der charakteristischen Alvar-Magerrasen erlauben. Möglicherweise vermindert aber die Zunahme an generalistischen Arten die Qualität der Alvar-Magerrasen durch relative Abnahme der Alvar-charakteristischen Pflanzenarten. Wenn die Büsche noch nicht ihre volle Größe erreicht haben oder es sich um Buschjungwuchs handelt, birgt Verbuschung immer auch die Gefahr des Größerwerdens der Büsche, was sich dann schnell negativ auf die Magerrasen auswirken kann. Auch die mit dem Alter der Büsche zunehmende Menge an produzierten Diasporen kann eine stabile leichte Verbuschung erschweren oder gar unmöglich machen. Nicht zuletzt schaffen Gebüsche mit ihrem Schattenwurf nicht nur Wuchsorte für mesophile Generalisten sondern auch *Safe sites* für die eigenen Nachkommen, oder sie breiten sich mit Hilfe von Polykormonen aus. Solche Eigendynamiken einer Verbuschung von Kalkmagerrasen dürfen nicht unterschätzt werden. Sie sind bisher nicht gut untersucht – dies sollte geändert werden.

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Supplements and Appendices

Appendix 1. Minimum, maximum, and mean values with standard deviation (SD) of environmental parameters, shrub cover, and different components of species richness used in structural equation modelling.

Anhang 1. Minimum, Maximum und Mittelwert mit Standardabweichung (SD) verschiedener Umweltparameter, dem Deckungsgrad holziger Arten und von verschiedenen Komponenten des Artenreichtums, die im Strukturgleichungsmodel verwendet wurden.

Parameter	N	Min	Max	Mean ± SD
Shrub cover (%)	33	0.00	32.20	8.31 ± 7.22
Soil depth (cm)	33	3.14	16.39	8.16 ± 3.29
CV of soil moisture	33	0.13	0.68	0.27 ± 0.12
CV of soil temperature	33	0.01	0.08	0.04 ± 0.01
CV of light availability	33	0.15	0.65	0.35 ± 0.11
CV of soil pH	33	0.01	0.06	0.04 ± 0.01
Total species richness	33	4.86	12.03	8.64 ± 1.85
Characteristic species richness	33	1.85	5.77	3.82 ± 0.85
Generalist species richness	33	1.81	7.27	4.82 ± 1.41

Appendix 2. Species lists of characteristic and generalist species found in the 33 studied alvar grasslands.

Anhang 2. Artenliste der charakteristischen und generalistischen Arten in den 33 untersuchten Alvar-Magerrasen.

Characteristic species

Acinos arvensis (Lam.) Dandy
Anemone sylvestris L.
Antennaria dioica (L.) Gaertn.
Anthyllis vulneraria L. s. l.
Artemisia rupestris L.
Asperula tinctoria L.
Astragalus danicus Retz.
Carex ornithopoda Willd. s. str.
Carlina vulgaris L. s. str.
Cirsium acaule Scop.
Daucus carota L.
Echium vulgare L.
Festuca ovina L. s. str.
Filipendula vulgaris Moench
Helianthemum nummularium (L.) Mill. s. l.
Helictotrichon pratense (L.) Besser
Lotus corniculatus L.
Medicago lupulina L.
Phleum phleoides (L.) H. Karst.
Pimpinella saxifraga L.
Plantago lanceolata L.
Potentilla neumanniana Rchb.
Prunella vulgaris L.
Ranunculus bulbosus L.
Scabiosa columbaria L.
Sedum acre L.
Sedum album L.
Thymus serpyllum L.
Trifolium montanum L.
Veronica spicata L.
Vincetoxicum hirundinaria Medik.
Viola rupestris F. W. Schmidt

Generalist species

Achillea millefolium L.
Agrimonia eupatoria L.
Alchemilla spp.
Arabis hirsuta (L.) Scop.
Artemisia campestris L.
Brachypodium pinnatum (L.) P. Beauv.
Briza media L.
Bromus hordeaceus L.
Campanula glomerata L.
Campanula persicifolia L.
Campanula rotundifolia L. s. str.
Carex caryophyllea Latourr.
Carex flacca Schreb.
Carex tomentosa L.
Centaurea jacea L. s. l.
Cerastium fontanum Baumg. s. str.
Cirsium vulgare (Savi) Ten.
Convallaria majalis L.
Convolvulus arvensis L.
Dactylis glomerata L.
Danthonia decumbens (L.) DC.
Erigeron acer L.
Euphrasia spp.
Festuca pratensis Huds. s. l.
Festuca rubra L.
Fragaria spp.
Galium album Mill.
Galium boreale L.
Galium verum L. s. str.
Leontodon autumnalis L.
Leontodon hispidus L.
Leucanthemum vulgare Lam. s. str.
Linum catharticum L.
Luzula spp.
Melampyrum arvense L.
Melampyrum pratense L.
Myosotis spp.
Origanum vulgare L.
Phleum pratense L. s. str.
Pilosella officinarum F.W. Schultz et Sch. Bip.
Pilosella spp.
Plantago maritima L.
Plantago media L.
Poa angustifolia L.
Poa compressa L.
Polygala comosa Schkuhr
Polygonatum odoratum (Mill.) Druce
Potentilla reptans L.
Primula veris L.
Pulsatilla pratensis (L.) Mill.
Ranunculus acris L.
Ranunculus polyanthemos L. s. str.
Rumex acetosa L.
Sagina nodosa (L.) Fenzl
Senecio jacobaea L.
Sesleria caerulea (L.) Ard.
Silene nutans L.
Silene vulgaris (Moench) Garcke

Geranium sanguineum L.
Gymnadenia conopsea (L.) R. Br.
Helictotrichon pubescens (Huds.) Pilg.
Hepatica nobilis Schreb.
Herminium monorchis (L.) R. Br.
Hieracium spp.
Hieracium umbellatum L.
Hypericum perforatum L.
Inula salicina L.
Knautia arvensis (L.) Coult. s. str.
Lathyrus pratensis L.
Solidago virgaurea L.
Taraxacum officinale F.H. Wigg. (coll.)
Trifolium medium L.
Trifolium pratense L.
Trifolium repens L.
Veronica chamaedrys L. s. l.
Veronica officinalis L.
Vicia cracca L.
Viola spp.
Viola collina Besser
Viola hirta L.

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