

Assembly of plant communities in grasslands

The importance of different filters

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by

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Summary

For plants to establish in a local community from a pool of possible colonizers from the region, it must pass through a series of filters. Which of the filters is most important in this process has been much debated. While some studies indicate that community assembly is highly deterministic, governed by species interactions others have suggested that species occurrence is mainly constrained by the ability of species to disperse to and establish at a site.

In this thesis I explore plant community assembly in grazed Swedish grasslands with the overall aim to determine which processes affect assembly in those habitats. I examined how plant functional trait diversity varied among and within communities of species-rich grasslands and species-poor ex-arable fields and how species are filtered from the regional species pool into ex-arable fields and if this filtering is linked to species functional traits.

There was little evidence of functional traits related to the established phase of plant life cycle affecting the assembly. Community assembly from the regional species pool into ex-arable fields was mostly influenced by factors that enhance the probability of species to disperse to a site. Semi-natural grasslands had higher species richness than ex-arable fields because they were older and thus have had longer time to accumulate species. There was a strong relationship between processes working on the regional scale (that determine regional richness and abundance) and community assembly on the local scale. The results strengthens the view that assembly of communities from a pool of suitable colonizers is strongly affected by the ability of species to disperse to a site.

List of papers

The thesis is based on the following manuscripts, referred to by their roman numerals:

- I. Marteinsdóttir, B. & Eriksson, O. Plant community assembly in semi-natural grasslands and ex-arable fields: a trait based approach. *Manuscript*.
- II. Marteinsdóttir, B. & Eriksson, O. Trait-based filtering from the regional species pool into local grassland communities. *Manuscript*.

Introduction

How plants are assembled into communities from a pool of potential colonizers has been one of the central debates in plant ecology for the past century. It dates back to the publications of Gleason (1926) and Clements (1916; 1936) in the beginning of the 20th century. Gleason (1926) had an individualistic approach and believed that communities were merely an assortment of species with similar adaptation to the environment, while Clements (1936) described communities as highly organized, constructed from mutually interdependent species. Today the debate lies between those that claim that plant occurrence is mostly random only constrained by the ability of species to disperse and withstand the current environmental conditions at a site (e.g. Hubbell 2001; Freestone & Inouye 2006) and those that argue that community assembly is highly deterministic often affected by the presence of other species in the community, i.e. assembly rules (Wilson & Roxburgh 1994; Fargione et al. 2003; Turnbull et al. 2005).

Assembly rules have been defined as ‘restrictions on species presences or abundance that is based on the presence or abundance of one or several other species or types of species (not simply the response of individual species to the environment)’ (Wilson & Gitay 1995). Limiting similarity and niche limitations are example of well known assembly rules. Limiting similarity implies that competition for resources has resulted in species divergence as competition is stronger between species that are more similar in their resource use (e.g. MacArthur & Levins 1967; Diamond 1975; Pacala & Tilman 1994). Niche limitation has been defined as the restriction on the ability of species to coexist within a finite area because of limitation in number of niches (Wilson et al. 1996). Environmental filtering can also cause non random community structure and occurs when certain species which lack traits for persisting under a particular set of abiotic conditions are filtered from the local community (Keddy 1992a). The unified neutral theory of biodiversity and biogeography (Hubbell 2001) is often used to explain random structure of communities. The theory assumes that species are ecological equivalents and processes affecting community level patterns are ecological drift (the relative change in species frequency due to chance), speciation and random dispersal. Dispersal limitations causes random assembly and occurs when species are lacking from suitable sites simply because they have not dispersed there (e.g. Zobel et al. 2000; Tofts & Silvertown 2002). Randomness can also occur

when community assembly is highly influenced by a stochastic arrival order of species into a site (i.e. priority effect *sensu* Almany 2003).

A vast number of studies have explored how grassland plant communities are constructed but their results have varied. While some have found evidence of assembly rules and nonrandom structure (e.g. Wilson & Roxburgh 1994; Fargione et al. 2003; Fukami et al. 2005; Questad & Foster 2008) others find no such patterns (e.g. Watkins & Wilson 1994; Schamp et al. 2008) or evidence of dispersal limitation (e.g. Zobel et al. 2000; Tofts & Silvertown 2002) influencing the assembly. It has been suggested that community assembly is strongly affected both by stochastic and deterministic factors, with environmental filtering and species dispersal controlling the assembly on larger scale but species interaction on smaller scale (e.g. Reitalu et al. 2008). It is difficult to compare results among studies as they use different approaches (experimental and descriptive), are done on different scales and use different measures to assess the community: for example species identity (e.g. Van der Maarel et al. 1995; Foster & Dickson 2004), guilds (e.g. Wilson & Roxburgh 1994; Wilson & Watkins 1994; Fargione et al. 2003) and functional traits (e.g. Matsui et al. 2002; Harpole & Tilman 2006; Ackerly & Cornwell 2007; Cornwell & Ackerly 2009). Even within the same study, using the same methods and estimates, results can vary both between different vegetation types (Matsui et al. 2002) and between adjacent sites of the same type (Sebastian 2004).

Species identity is commonly used in assembly studies (e.g. Ruprecht et al. 2007; Reitalu et al. 2008) but the large number of species makes the detection of patterns difficult and the results site specific. It is therefore hard to detect any common patterns or rules and the results have limited generality (Keddy 1992a; Keddy 1992b). Guilds condense species lists by grouping species according to similarities in selected characteristics that might be ecologically relevant (e.g. Wilson 1999), thus linking observed patterns to function of the ecosystem and making results comparable among sites (Wilson 1999; Brown 2004). Species functional traits are measured on the species level where species with similar traits are assumed to occupy similar niches, have similar functional roles and respond similarly to the environment (Lavorel et al. 2007; Violle & Jiang 2009). One of the largest gain of using functional traits in assembly studies is that it makes

ecology a more predictable science (e.g. Weiher & Keddy 1995; McGill et al. 2006; Shipley 2009) without losing detail.

Dispersion of traits and guilds in communities may show random distribution (e.g. Watkins & Wilson 2003), divergence or convergence (Grime 2006). Divergence is seen as evidence for competition for resources (e.g. Weiher & Keddy 1995; Weiher et al. 1998) with stronger competition between species with similar traits. Thus species must differ from other species in the community (i.e. limiting similarity), in order to coexist (MacArthur & Levins 1967; Diamond 1975; Pacala & Tilman 1994). Convergence indicates environmental filtering as only species with certain traits that enables them to tolerate the site abiotic conditions are able to establish and grow (e.g. Keddy 1992a; Weiher & Keddy 1995).

One of the difficulties with studying community assembly is the historical legacy of many ecosystems. Therefore the species assembly is not only affected by current local and regional conditions but also those in the past. Grasslands that have developed on grazed ex-arable fields are often young habitats with short historical legacy. They are therefore highly suitable for studies on community assembly. Semi-natural grasslands often occur in the same landscape but in contrast to ex-arable fields they usually have a long history (Cousins & Eriksson 2002; Eriksson et al. 2002) and are species rich (e.g. Kull & Zobel 1991; Cousins & Eriksson 2002). The high species richness is thought to be an effect of large historical areas, management continuity, constant disturbance by grazing animals and current and past propagule pressure from the region (Janssens et al. 1998; Cousins & Eriksson 2002; Eriksson et al. 2002; Eriksson et al. 2006). Thus comparing those two grasslands types gives an opportunity to explore the influence of historical legacy in plant community assembly.

Objectives

In this thesis I explore plant community assembly in grazed Swedish grasslands with the overall aim to determine which processes affect assembly in those habitats. In paper **I**, I examined how plant functional trait diversity varied among and within communities of species-rich semi-natural grasslands and species-poor ex-arable fields. My specific questions were:

- Can differences in species assembly between semi-natural grasslands and ex-arable fields be explained by variation in functional traits or/and environmental factors?
- Is assembly of traits at the study sites more determined by deterministic factors like assembly rules and environmental filtering or stochastic factors like dispersal limitation?

In paper **II**, I explored how species are filtered from the regional species pool into ex-arable fields and if this filtering is linked to species functional traits. Especially I asked:

- Is there a connection between species richness in the regional species pool and species richness in the target grasslands?
- Can differences in species abundance and functional traits explain which species from the regional species pool will establish at the ex-arable fields?

Further studies will focus on how current and previous landscape features surrounding the target sites affect the community assembly, explore the importance of seed- and niche limitations using an experimental approach and assess the significance of incoming seed rain and clonal growth in the assembly process.

Materials and methods

Study area

The study took place in and near Nynäs nature reserve, southeastern Sweden (58°49'N, 17°24'W). The landscape is a mosaic of arable fields, semi-natural grasslands, ex-arable fields and forest (Cousins & Eriksson 2002). The study sites were species-rich semi-natural grasslands and species-poor ex-arable fields. All sites were grazed with livestock (sheep or cattle).

Methods

In paper **I** plant species abundance was estimated in six ex-arable fields and eight semi-natural grasslands. Soil samples were collected from each site and analyzed for pH, P, NH₄⁺, K, Ca, Mg and soil moisture content. We measured three plant functional traits (specific leaf area (SLA; mm²/mg), leaf dry matter content (LDMC, mg/g) and seed mass (mg)) by collecting leaves and

seeds from each site where species occurred. SLA, LDMC and seed mass were then measured in the lab using the guidelines in Cornelissen et al. (2003).

In paper **II**, plant species abundance was measured in four study plots located within 12 ex-arable fields. Commonness and presence of flowers and/or fruits of each species was recorded in a 100 m radius around the center of each site (including the abundance plots). The regional species pool was then determined as the set of species found in the total species pool that should be able to grow in ex-arable fields, the regional propagule pool as the species in the regional pool that were found flowering or with fruits and the local pool as all the species found within the four study plots within each site. To examine if species traits affected the filtering of species from the regional pool into the local pool the following traits were used: mean seed mass (mg), mean height (mm), clonal growth index and dispersal vector.

Nomenclature follows Mossberg and Stenberg (2003).

Data analysis

In paper **I** differences in environmental factors, mean site trait values and species richness between semi-natural grassland and ex-arable fields were explored with a Wilcoxon rank sum test. Nonmetric multidimensional scaling (NMDS) with site soil attributes fitted to the scaling was used to investigate how species were arranged into sites. Trait-gradient analysis (Ackerly & Cornwell 2007) that partitions species trait values into α -(within-community) and β -(among-communities) components was applied to abundance weighted species trait data and the relative niche breadth of each species calculated as the range of site mean trait values in sites where it occurs. A null model of community assembly was used to explore if species were assigned to sites at random according to their α - and β -trait values. Pearson's product moment correlation was used to estimate correlations among the three traits in species mean trait values and the relationship between mean log species abundance and species mean trait values. Spearman rank test was used to estimate correlation between site mean trait values and between site mean trait values and soil properties and total site species richness.

In paper **II** site mean trait values, site trait variance and site mean nearest trait distance (meanNTD) were calculated for the local species pool at each site. Monte Carlo simulations were

used to test if relationships between species richness of different scales were stronger than expected by random (see Pärtel et al. 1996; Pärtel & Zobel 1999) and to determine if species traits (mean values, variance and meanNTD) influenced the filtering of species from the regional species pool into local communities. Relationship between species abundance on the regional and the local scale were examined using Spearman's rank correlation.

Statistical analyses were conducted using R 2.8.1. and 2.10.1. for Windows (available from <http://cran.r-project.org>) with the additional package Vegan and MASS.

Results and discussions

Paper I

There was a much higher species richness in semi-natural grasslands (58 ± 1.65 species) than in ex-arable fields (22 ± 3.93 species; $t_{6,8,14} = -8.56$, $p < 0.001$) and the species composition differed between the two grassland types, with semi-natural grassland being less variable than ex-arable fields (Fig. 1).

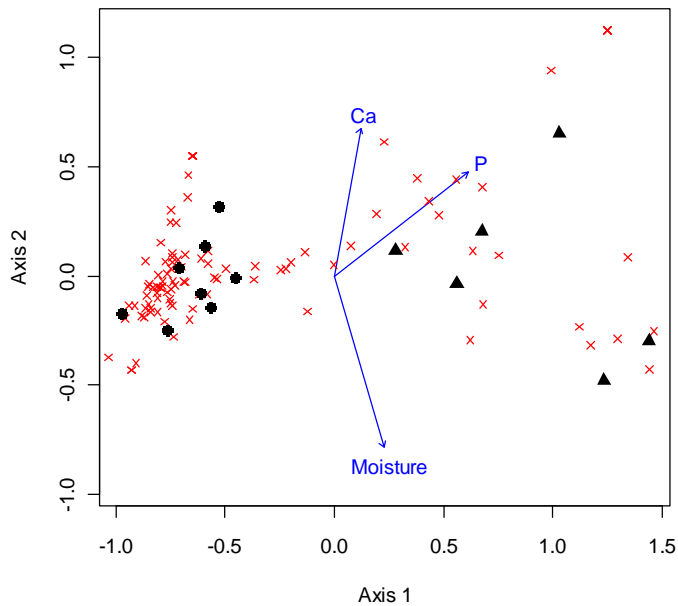


Figure 1. Distribution of species in eight semi-natural grasslands and on six ex-arable fields in Nynäs nature reserve showed in a nonmetric multidimensional scaling (NMDS) diagram. Ex-arable sites are marked with triangles, semi-natural grasslands with dots and species with crosses. Environmental variables were fitted onto the data after the scaling. Only significant variables are showed on the graph; Moisture: soil moisture; Ca: soil calcium and P: soil phosphorus.

The only significant difference in species traits and soil factors found between the two grassland types was a lower average seed mass of species in ex-arable fields ($W=3.00$, $p=0.005$; Fig. 2). Ex-arable fields are “young” communities and it is likely that species that have small seeds, which are produced in larger quantities (e.g. Jakobsson & Eriksson 2000; Kahmen & Poschlod 2008), are quicker to colonize them, than species that produce few but large seeds. Semi-natural grasslands on the other hand have accumulated species over many centuries of grassland management (Eriksson et al. 2002) and therefore most species in the region that can grow there have had time to disperse and establish. The species richness is thus higher and the species composition more similar among different semi-natural grassland sites, than among ex-arable fields.

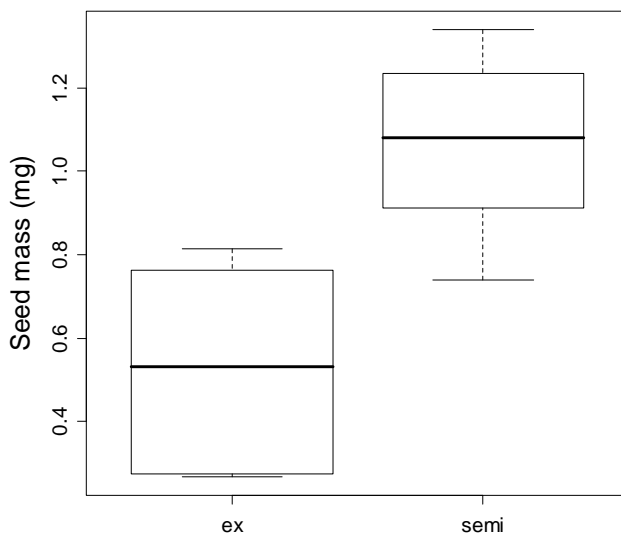


Figure 2. Abundance weighted site mean seed mass (mg) in eight semi-natural grasslands (semi) and on six ex-arable fields (ex) in Nynäs nature reserve. Horizontal line = median; box = data with upper and lower quartiles; ends of vertical lines highest and lowest data points.

Species were aggregated into sites depending on their seed mass, species had higher or lower α - and β -values than expected by random and many species had intermediate niche breadth values concerning their seed mass (Fig. 3c), indicating that each species had a restricted range of site it grew in. This is consistent with our conclusions that larger seeded species are more often found in semi-natural grasslands.

Traits linked to the established phase of plant life cycle (LDMC and SLA) were however randomly distributed among the sites, thus no indication of limiting similarity caused by species interactions were found. No evidence of environmental filtering was found as most species had wide niche breadth concerning those traits (Fig. 3a,b), indicating that they could grow at majority of sites.

Results of other studies have demonstrated that once established, plant fitness is independent of seed size (Eisenhauer & Scheu 2008) which is consistent with our results as no relationship was found between seed mass and species abundance. High correlation between species abundance and species LDMC and SLA ($r=0.27$, $p=0.03$ and $r=-0.29$, $p=0.02$, respectively) suggests that even though functional traits related to the established phase of the life cycle do not affect which species are present at a site they still have some influence on abundance patterns (c.f. Reader 1998).

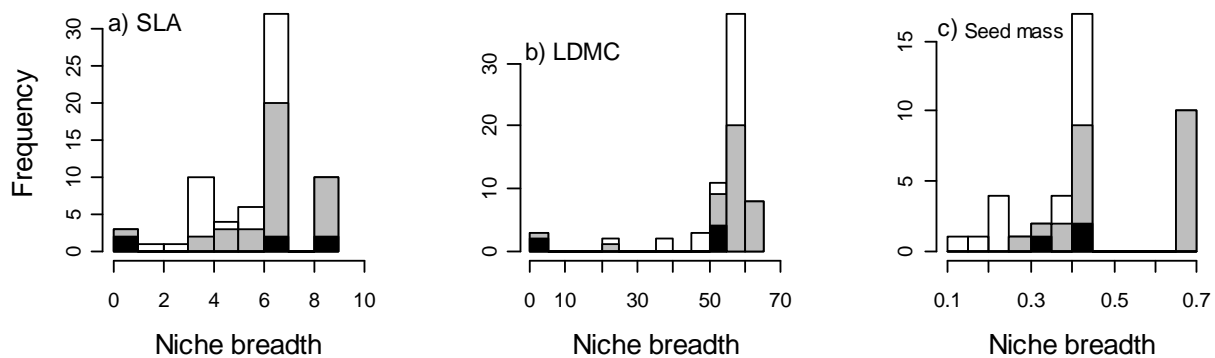


Figure 3. Niche breadth of plant species traits a) SLA (mm^2/mg), b) LDMC (mg/g) and c) log seed mass (mg) measured from six ex-arable fields and eight semi-natural grasslands in Nynäs nature reserve. Black bars represent frequency for species only occurring in ex-arable fields, gray species occurring in both environments and white species only in semi-natural grasslands.

Paper II

Despite that only a small part of the regional species pool was found growing in each ex-arable field site (average 28%), local species richness was positively affected by species richness in the regional species pool ($r=0.88$, $p=0.001$; Fig.4), which is consistent with other results from grassland communities (Pärtel et al. 1996; Pärtel & Zobel 1999). Thus evolutionary and historical processes that are responsible for the formation of the regional species pool are of primary importance in determining the level of local species richness (Ricklefs 1987; Cornell & Lawton 1992; Eriksson 1993).

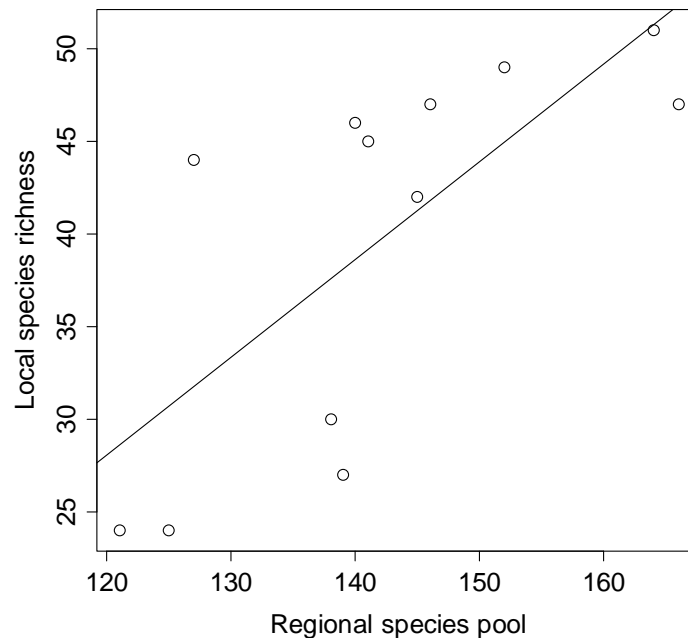


Figure 4. Relationship between the regional species pool (100 radius area) and local species richness at 12 ex-arable field sites in Nynäs nature reserve, SE-Sweden.

We found no evidence for trait convergence or divergence (Table 1 & 2) for height which is connected to species competition abilities (Lamb et al. 2006) or clonal ability which is connected to species persistence (Ozinga et al. 2007; Johansson et al. *in press*).

Table 1. The proportion of 4999 randomly derived site mean trait values that were higher or lower (-) than the observed mean site trait values derived from each of the 12 ex-arable field sites in Nynäs nature reserve, SE-Sweden. The traits used were species abundance in the regional species pool, mean height, seed mass, clonal growth index (CGI) and dispersal method (proportion with unassisted dispersal). This was done both for pure values (N) and where values were weighted with the species abundance in the total species pool (W). Bold values represent incidents where the observed mean site trait value was significantly ($p < 0.025$) higher or lower (-) than expected from random.

Site	Abundance	Height		Seed mass		Dispersal method		CGI	
		N	W	N	W	N	W	N	W
Langmaren	>0.001	-0.223	-0.152	-0.240	-0.276	0.011	0.003	0.400	-0.378
Langmarenmyr	>0.001	0.190	0.482	-0.295	0.484	0.243	0.008	0.027	0.450
Langmarenpark	>0.001	-0.153	-0.368	-0.404	-0.421	0.001	>0.001	0.220	0.323
Lindviken	>0.001	-0.128	-0.172	0.210	0.394	0.022	0.004	0.369	-0.465
Lindvikenaker	0.020	0.371	0.408	0.197	0.329	0.017	0.020	0.041	0.047
LitselbyA	>0.001	-0.066	-0.377	-0.136	0.500	0.050	0.008	0.030	0.142
LitselbyB	0.002	-0.173	0.434	-0.288	-0.468	0.022	0.004	0.059	0.295
Mellanstugan	>0.001	0.001	0.025	0.335	0.409	0.019	0.008	0.342	0.454
Nyckelbykulle	>0.001	0.436	0.394	0.173	0.374	0.044	0.008	0.029	0.145
Nyckelby	>0.001	0.051	0.119	0.049	0.228	0.126	0.018	0.033	0.175
SandvikenA	>0.001	-0.444	0.335	0.360	0.442	0.060	>0.001	0.223	0.437
SandvikenB	>0.001	0.319	0.215	0.438	-0.492	0.002	0.001	0.013	0.016

If the ability of species to disperse to a site is the main filter influencing community assembly (i.e. dispersal limitation) we would expect a positive relationship between the ability of species to disperse to a site and its occurrence in ex-arable fields. Species seed mass, which has been associated with seed production (e.g. Jakobsson & Eriksson 2000; Moles & Westoby 2004) and dispersal abilities (Cornelissen et al. 2003), did not affect the filtering process (Table 1 & 2). For all sites, species that were abundant in the regional species pool were however more likely to be found in the local species pool (Table 1) and there was a positive relationship between local and regional species abundance (all species: $r=0.47$, $p<0.001$, only local species: $r=0.41$, $p<0.001$). Bell (2001) suggested that the fact that abundant (rare) species at one site are also abundant (rare) on others could be explained with neutral community ecology, as abundant species are more likely to disperse to new sites. Dispersal method was also impacting species filtering, with species with unassisted dispersal more likely to be found in ex-arable fields than expected by random (Table 1). Seeds of grasses and dicots with unassisted dispersal are frequently consumed by herbivores along with the leaves of their parent plant (Janzen 1984), and in grazed grasslands,

this mode of dispersal is important (Pakeman et al. 2002; Traba et al. 2003; Kuiters & Huiskes 2010) and can probably explain the increased dispersal abilities of those species.

Table 2. The proportion of 4999 randomly derived site trait variance (*var*) and mean nearest trait distance (NTD) that were higher or lower (-) than the observed values derived from each of 12 ex-arable field sites in Nynäs nature reserve, SE-Sweden. The traits used were species abundance in the regional species pool, mean height, seed mass and clonal growth index (CGI). Bold values represent incidents where the observed site value was significantly ($p < 0.025$) higher or lower (-) than expected from random.

	Abundance		Height		Seed mass		CGI
	<i>var</i>	NTD	<i>var</i>	NTD	<i>var</i>	NTD	<i>var</i>
Langmaren	0.297	0.083	-0.020	-0.163	0.308	-0.387	0.225
Langmarenmyr	-0.247	0.141	0.382	0.272	0.491	-0.484	0.413
Langmarenpark	-0.089	0.106	-0.030	-0.105	0.422	-0.399	0.195
Lindviken	0.425	0.046	-0.004	-0.019	0.339	0.099	-0.283
Lindvikenaker	0.126	0.047	-0.032	-0.263	0.218	0.252	0.216
LitselbyA	0.383	0.251	-0.015	-0.198	0.318	-0.379	-0.302
LitselbyB	-0.390	0.277	-0.097	-0.132	-0.369	-0.325	-0.409
Mellanstugan	-0.431	-0.380	-0.419	0.033	-0.461	0.491	0.372
Nyckelbykulle	-0.425	0.458	-0.132	-0.183	0.358	0.287	0.315
Nyckelby	-0.397	-0.114	-0.152	0.401	0.200	0.144	0.397
SandvikenA	0.100	-0.198	-0.055	-0.183	-0.472	0.486	0.379
SandvikenB	-0.116	0.002	-0.068	-0.410	0.394	0.476	0.280

Conclusions and further studies

Dispersal limitation is an important factor in community assembly in grazed grasslands, the older the grasslands the higher the probability of species to colonize the site and therefore we found higher species richness in semi-natural grasslands. Community assembly in grazed grasslands is also affected by processes on the regional scale, with regional species richness and abundance highly influencing the local species assembly. Our results strengthens the view that assembly of communities from a pool of suitable colonizers is strongly affected by the ability of species to disperse to a site (e.g. Gleason 1926; Hubbell 2001), at least at sites under constant disturbance like grazed grasslands.

The limitations of using models and descriptive data to determine species assembly have been discussed by some authors (Van der Maarel et al. 1995) who emphasized that experiments are needed to answer this question. We agree and in future studies we will use experiments to verify

our results, based on descriptive data. We will also look more closely on the relationship between local community assembly and the regional landscape.

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