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Exploring the relationship between species richness and intraspecific trait variability

Bachelor thesis

Hana Dvořáková

Supervisor: Doc. Francesco de Bello, Ph.D.

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Annotation:

This thesis was originated as a contribution to the wide range of biodiversity studies published recently. It focused on the little explored importance of intraspecific variability in plant communities. A pot experiment hold in glasshouse environment was designed to observe influence of biotic interactions in mixtures of various species diversity on species functional traits and productivity. Variability of functional traits of individual species was assessed in relation to increasing species richness and the contribution of within-species variance to the total variance of pot communities was evaluated at different richness levels.

I hereby declare that this bachelor thesis is entirely the result of my own work. I have only used the resources given in the list of references.

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Hana Dvořáková

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1. Introduction

In the last decades the global loss of diversity due to climate changes and growing human influence has become a major concern not only of ecologists but also of the general public (Lepš, 2005; Millenium Ecosystem Assessment, 2005). The new flurry of ecological research on the effect of biodiversity on ecosystem function brought many questions about the real impact of the diversity loss and its consequences on ecosystem functioning from both scientific and economical points of view (Srivastava and Vellend, 2005). Addressing these questions requires a common framework of reference of terminology to evaluate the problematic more efficiently.

In the past two decades, it has become evident that the effect of biodiversity on ecosystem processes is not mediated by species richness alone, but rather by the functional characteristics of species (Hooper *et al.,* 2005; de Bello *et al.,* 2010). These characteristics are called functional traits and refer to morphological, physiological and life-history properties of plants that can directly or indirectly influence their fitness and competitive ability (Violle *et al.,* 2007). Nevertheless, one important aspect of functional traits, the intraspecific variability, and its potential effects on species coexistence and ecosystem functioning, has been receiving relatively small attention. The importance of intraspecific variability for local species coexistence was recognised decades ago (Mac Arthur and Levins, 1967) but despite the cognizance of existence of potentially wide within-population variation it has been neglected over time in community ecology (Violle *et al.,* 2012). However, as the problematic of climate changes has raised the public interest in the biodiversity-ecosystem function research, new developments in trait-based community ecology underlined the need to integrate influence of both intraspecific and interspecific variation in the community ecology research (Violle *et al.,* 2012). In this thesis, key concepts and publications regarding studies on biodiversity, ecosystem functioning and their connections to experiential approaches have been revised and summarized. Then it is explained how the importance of functional diversity, and particularly intraspecific trait variability, in species interactions and productivity could be taken into account using a pot experiment as a case study.

1.1. Species diversity and ecosystem functioning

Biodiversity does not only mean the number of species on a delimited area, this term also implies differences between a community of equally represented individuals and a community where few strong species dominate even if both of them are composed of the same total number of species. For that reason, two basic components of biodiversity are distinguished: species richness and evenness of species relative abundances that is usually expressed as the ratio of the actual diversity and the maximum possible diversity for a given number of species (Lepš, 2005). The biodiversity-ecosystem function literature clearly separates effects of species diversity and effects of composition on community functioning (Srivastava and Vellend, 2005).

Ecosystem functioning is a complex concept, which makes it problematic to evaluate. Its function is often related to human needs and expected ecosystem services defined by Daily (1997) as 'the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life'. This view indicates underlying assumptions that particular qualities of an ecosystem are considered better than others and these qualities can differ significantly among managed ecosystems with various agricultural purposes. Ecologists attempt to adopt a more objective stance. Naeem et al. (1999) defined functioning as simply showing activity and a more focused concept was suggested by Pacala and Kinzig (2002), who distinguished three classes of ecosystem functioning: 1) stocks of energy and materials, 2) fluxes of energy or material processing, and 3) stability of rates or stocks over time (Srivastava and Vellend, 2005). Nevertheless the most frequently used parameter of ecosystem functioning is productivity, usually measured as standing crop biomass, which is relatively easy to measure and in many experiments represents a very reasonable characteristic often correlated with other functional characteristics such as nutrient retention or CO_2 assimilation (Lepš, 2005).

Although considerable amount of data has been compiled since the new boom of biodiversity research, their presentation is often based on the old idea of diversity being the root of ecosystem functioning (Lepš, 2004). This point of view has caused disagreements among ecologists (Naem *et al.,* 1999; Wardle *et al.,* 2000; Kaiser, 2000) as the interpretation of the obtained data is dependent on the experimental approach applied. As Schmid (2002) indicates, there are two basic ways to study the relationship between diversity and ecosystem functioning. First, natural communities can be studied investigating the correlation between

diversity and their functioning. Second, biodiversity experiments with manipulated diversities can be established and functioning measured as a response or species can be removed from existing natural communities. In the first case, the environmental conditions of the habitat, the common factor that affects both diversity and ecosystem functioning, need to be considered. In the second case, the experiments involve random selection of species included or excluded from the community, which does not correspond to real ecosystems, where assemblages of species are usually formed non-randomly (Lepš, 2004). In other words, in real communities it is not as important how many species are lost as which species are lost (Aarssen, 2001). In a previous study, species' tendency to go extinct depending on their functional qualities, particularly on their indicator values for nitrogen (i.e. the preference of species for habitats with different levels of nutrient availability) was proposed as a main trend (Ellenberg, 1985). It well matches the field experience of species being outcompeted as a result of eutrophication. However, this situation disproves the hypothesis that loss of diversity needs to result in productivity decrease (Lepš, 2004).

Several experiments show clear positive relationship between species richness and productivity. One of them, established as a part of 'The Jena Experiment' in Germany, focused on two goals – testing influence of scale effects by manipulating plot size and influence of exclusion of subordinate species from the community on the richness-productivity relationship. At both spatial scales used in the experiment identical positive relationship between diversity and productivity was found suggesting the possibility to predict functions of greater communities on the basis of local experiments, at least over a short time period. The other part of the experiment also brought interesting results. Biomass production was higher in the assemblages of dominant species compared to that of both dominant and subdominant ones, as expected, but the difference was larger for mixtures than for monocultures. Greater increase in production of mixtures composed of only dominant species compared to monocultures indicates stronger intraspecific than interspecific competition of the dominant species. This study also considers two important components of productivity, i.e. the 'complementarity effect', a facilitation of species co-existence due to their various functional traits, and the 'selection effect', an improved production of a community as a result of dominance of one of the species (see also below). Both these components were positive in all cases, yet also significantly stronger in the dominant species assemblages, complementarity showing curvilinear dependence reaching maximum at low species levels (4-6), selection increasing linearly (Roscher *et al.,* 2005).

Two meta-analyses of biodiversity studies also found random reductions of species richness resulting, on average, in decline of ecosystem functioning (Balvanera *et al.,* 2006 and Cardinale *et al.,* 2006). Based on these meta-analyses, five hypotheses were tested (Schmid *et al.,* 2009). The first one: 'various ecosystem types are affected by biodiversity differently' (Hooper *et al.,* 2005) was supported; however a great similarity between terrestrial and aquatic ecosystems was found. The second: 'species richness intensifies community responses but weakens responses of populations' (Balvanera *et al.,* 2006) was also confirmed backing arguments about density compensation (McGrady-Steed and Morin, 2000). The test of the third hypothesis showed that biodiversity influences standing stocks more strongly and more positively than depletion of resources. The fourth hypothesis about predictions that increased biodiversity at one trophic level reduces functions at other trophic levels but enhances functions on the same trophic level proved to be right, except mostly positive bottom-up effects on detritivore functions. Also the fifth hypothesis that increasing biodiversity should prevent invasion was strongly supported by one of the analyses but there are some speculations about generality of this result (Schmid *et al.,* 2009).

Productivity is often used as a measure of ecosystem functioning (Lepš, 2004). However, there has been frequently found a unimodal relationship between species richness and productivity. The increasing part of the dependence is fairly expectable; ecologists were rather confused by the other side of the hump, where the diversity decreases with growing productivity and lowering levels of disturbance. The most frequent explanation for present-day semi-natural and natural European grasslands is the influence of eutrophication. The increased nutrient load is often found to cause loss of oligotrophic species due to strong dominance of few highly productive species (Lepš, 2005). This process is called 'selection effect' and presents one component of the additive partitioning method by Loreau and Hector (2001).

A new method called additive partitioning method was developed in 2001 to solve the controversy about diversity-productivity experiments caused by participation of two processes operating in combination. First, it separates the 'selection effect', when species with particular traits dominate the community and control its functioning. The diversity-productivity relationship is then positive, when the dominant species are also highly productive and increased species richness means higher probability of including these species. The second, 'complementarity effect' is composed of niche differentiation and facilitation effects and is able to increase the community performance above those expected

from individual species by their cooperation. The net biodiversity effect sums two preceding to show the deviance of the mixture yield from the values expected on the basis of monocultures and relative species abundance (Loreau and Hector, 2001).

1.2. Functional diversity and coexistence

The concept of diversity has been often simplified just to the number of present species and its other components such as trait variability between and within species and their proportional representation have been generally less studied. However, in the last decade there has developed an integrated idea of the value and range of species traits being the strong determinants of ecosystem functioning, often independently of the number of species (Díaz and Cabido, 2001). This idea symbolizes the recently recognized difference between species and functional diversity and points out the need to include the effect of presence of various functional groups in the concept of functional diversity. The hierarchy as the diversity of functional groups and species diversity within these groups then can be described (Lepš, 2005). More recently, several authors have separated functional diversity in a community into components of within vs. between species trait dissimilarity (Lepš, 2005; Gubsch et al., 2011; Burns and Strauss, 2012; Violle et al., 2012; Le Bagousse-Pinguet 2014). It is expected that the increase in between-species functional diversity will allow species to exploit different niches, decrease competition between them and therefore increase productivity. At the same time, Violle *et al.* (2012) also highlights the fact that competition can be modulated by the way intraspecific variability changes with species diversity, causing more or less overlap between species (see next section).

The competitive exclusion principle, also known as Gause's principle, proposes that two species competing for the same resources cannot share the same niche, at least not in long term. One of the species is always supposed to be weaker and so outcompeted to the extinction or to a shift of its ecological niche (Gause, 1934). However, laboratory experiments have shown the species with nearly identical ecological strategies were able to live in an unvarying environment for long periods (Miller, 1967). It was supposed that in field conditions the chance of species' coexistence was determined by the rate of natural ecosystem fluctuations. The limiting value of species niche overlap was recognized as the d/σ ratio, d referring to interspecific variance in niche means and σ to intraspecific niche widths, ranging from 1 to 2 (May and MacArthur, 1972). Such model of 'limiting similarity'

states that if two species are more similar than some limiting value L, the third species will converge to the nearer of the two original competitor and if the two species are less similar than L, the third species will evolve an intermediate phenotype (MacArthur and Levins, 1967). In a simple way limiting similarity concept asserts that species need to be functionally different to coexist and not be outcompeted. Recently, several researchers have used between-species functional diversity to understand limiting similarity and coexistence mechanisms (Götzenberger *et al.,* 2012). But as it was indicated earlier, between-species trait variability is not the only mechanism enabling species co-existence and reducing competition.

1.3. The intraspecific trait diversity: new emphasis on this topic

Mac Arthur and Levins 1967 presented a ratio d/σ that was regarded as a resolution of Gause's principle, which declares that two species using the same resources are unable to live in one niche in equilibrium. The numerator d referred to interspecific differences in niche means, while the denominator σ represented intraspecific niche widths. Nevertheless, the role of σ stayed diminished until 1990s and only d was considered to be the key promoter of diversity. For a long time trait-based community ecology has built on the mean field theory, which is restricted to differences between mean trait values of co-existing species (Violle *et al.,* 2012). McGill *et al.* (2006) even stated that 'to be useful to community ecology, traits should vary more between than within species'. However, results of recent studies measuring values for all individuals in community have questioned this approach and suggested to base community ecology on individuals as they are in the direct interaction with the biotic and abiotic environment (Violle *et al.,* 2012).

Most literature on functional traits has been based so far on comparing mean values of co-existing species, neglecting the ability of individuals within one population to exhibit trait plasticity or different ecological strategies, which enable them to cope with the intra- and interspecific competition at least partly (Violle *et al.,* 2012). This approach results in underestimating the degree of niche and trait overlap between species (Courbaud et al., 2012)**.** Trait plasticity arises from genetically based variation and from environmental influences on gene expression (Burns and Strauss, 2012) and it poses the possibility for individuals to adjust changes in environmental conditions and succeed better in intra- and

inter-specific competition. Considering the functional trait variability is therefore essential for understanding community assemblages and function (Gubsch *et al.,* 2011; Le Bagousse-Pinguet, 2014).

The importance of intraspecific variability for species coexistence can be illustrated with the study of Burns and Strauss (2012), which besides positive effect of phylogenetic distance of competitors on community productivity presents phenotypic plasticity in trait divergence, particularly divergence in root:shoot ratio, as a substantial component enabling plant species to coexist and possibly even able to decrease phylogenetic signal in a community. Similarly, Gubsch et al. (2011) who tested 12 closely related species of grasses on trait acquisition to light and nitrogen, provided evidence that plant diversity results in significantly different trait expression even among phylogenetically close related grasses helping them to coexist in species-rich grass communities through niche partitioning. These results are bolstered by the existence of other studies reporting substantial trait variation among taxonomically and phylogenetically related species exposed to differing environmental conditions and disturbance (e.g. Craine *et al,.* 2001; Díaz *et al.,* 2007; Pontes *et al.,* 2010).

Once the importance of intraspecific variance is clear, the need to incorporate it in the community ecology meaningfully arises. A simple approach based on the existence of two kinds of filters, external and internal, allowing species to enter the community was proposed by Violle *et al.* (2012). However, these filters are not supposed to operate only on the mean values of species traits but also at the individual level. The external filters let in individuals with trait values close to an optimal trait value determined by external conditions. The internal filters are mostly governed by density-dependent processes such as competition that favour individuals with trait values different from the optimal one. The final spread of trait values of the individuals in the community around the optimal value depends on the rate of strength of these two filters. And as there can be distinguished four organizational levels of a community assembly, individual, population, community and regional pool, there are also six components of variance identified among these hierarchical levels: σ_{IP}^2, variation of trait values among individuals within population, σ_{PC}^2, variation of population mean trait values within community, σ_{CR}^2, variation of community mean trait values within regional pool, σ_{IC}^2, variation of trait values among individuals within community, σ_{PR}^2, variation of population mean trait values within regional pool and σ_{IR}^2, variation of trait values among individuals within regional pool. Ratios of these variances were labelled T ('T' for trait) and serve as

statistics quantifying the importance of external and internal filtering at various hierarchical levels. The most important three of them are $T_{IP/IC}$, $T_{IC/IR}$ and $T_{PC/PR}$. Particularly, the ratio $T_{IP/IC}$ shows variance within one population relative to variance over all species in the community and it responds to the strength of internal filters. The relationship between $T_{IP/IC}$ and local species diversity can then highlight the importance of different classical ecological theories. According to niche-based theory each species uses a fraction of available resources and this fraction is the smaller, the more species are there to compete for resources. Here the lower community-wide intraspecific variation $T_{IP/IC}$ means smaller niche widths of species and so higher possible diversity. The neutral theory of biodiversity expects equivalence among species resulting in no relation of $T_{IP/IC}$ to species diversity. Finally, there are 'individual variation' theories, which recognize intraspecific variation as the main driver of diversity and predict species diversity to grow with increasing $T_{IP/IC}$. The variance within community relative to total variance of regional pool measures the strength of external filters and can be evaluated in two ways considering trait values of all individuals in the community and regional pool, $T_{IC/IR}$, or taking into account only the mean values of all populations in community and regional pool, $T_{PC/PR}$. The comparison of these two statistics indicates whether filtering processes act on species level ($T_{IC/IR} < T_{PC/PR}$) as suggested in the mean field approach or on individual level ($T_{IC/IR} > T_{PC/PR}$) (Violle *et al.,* 2012).

1.4. Approach and concept of this thesis

The concept of this thesis was inspired by Violle et al. (2012)'s framework offering three possible shapes of the relationship between $T_{IP/IC}$ and species richness according to various ecological theories (see the previous section). On the basis of this framework, this thesis aimed to test the basic principles of species co-existence on a simple pot experiment in glasshouse conditions. For this purpose six common meadow species *Lychnis flos-cuculi, Achillea millefolium, Prunella vulgaris, Agrostis tenuis, Holcus lanatus* and *Festuca rubra* were used, sown in all possible combinations from monocultures to six species mixtures and grown in a glasshouse for 3 months under equal conditions. Four key functional traits related to competitive abilities and resource uptake were measured (biomass, height, specific leaf area and leaf dry matter content) to evaluate the productivity and prosperity of species growing in various species richness and combinations. Therefore, in this thesis the following objectives were proposed: 1) to investigate the response of functional traits and their

variability to species richness and biodiversity effects (net effect, complementarity effect and selection effect) at the level of individual species, 2) to explore the importance of intraspecific trait variability in whole (pot) communities and its trends in relation to changing species richness and corresponding biodiversity effects.

2. Methods

2.1. Experiment design and plant species used

The diversity experiment was established as a glasshouse pot experiment focused on studying intra- and inter-specific interactions in various mixtures of six plants species common for Czech meadows. The species were chosen according to following characteristics. It was looked (1) for species that naturally can grow together to build the experiment on realistic bases, (2) for species of at least comparable height, if possible, to minimize strong differences in competition for light, (3) for plants that are easy to grow and last but not the least (4) for the species of good germination. Due to the last criteria a germination test, previously to the diversity experiment, was done to choose the six best candidates of twelve originally proposed. It was decided to represent two plant groups equally in the experiment – dicotyledonous forbs and grasses. Following these requirements *Lychnis flos-cuculi, Achillea millefolium* and *Prunella vulgaris* were chosen as forbs and *Agrostis tenuis, Holcus lanatus* and *Festuca rubra* for grasses. All the seeds were supplied by the company Planta naturalis.

To avoid the complex set of factors impacting natural ecosystems such as heterogeneity of the environment, variability in spatial scales, time of establishment, environmental influences on gene expression and others, a pot experiment in a glasshouse therefore controlling for these factors was designed. The design of the experiment was suggested as it follows. All possible combinations on each richness level (1-6) were considered, each combination having an appropriate number of replicates. The intended total density in each pot was 60 individuals with each species of the mixture represented equally. Therefore, the sowing densities were a bit higher, proportional to the germination ratios gained from the germination test. Monocultures were established with two different densities, one corresponding to the densities of the mixtures (60 individuals per pot) and another one being lower (up to 10 individuals). The total number of pots was 186 (Table I.)

Table I.: Summary of the experimental design.

Number of species	Individuals per pot	Combinations	Replicates	Pots per diversity level
1	60	6	4	24
1	≤ 10	6	6	36
2	60	15	2	30
3	60	20	2	40
4	60	15	2	30
5	60	6	3	18
6	60	1	8	8
Total number of pots				186

The sowing was done on the 15th April 2014, using a mixture of gardening substrate (Table II.) and sand in a ratio of 3:1. Pots of the volume of two liters and upper dimensions 20x20 cm were placed in a glasshouse and watered and weeded regularly.

During the initial weeks of the experiment, a germination problem with *Prunella vulgaris* occurred, despite the fact that it germinated well in the preliminary germination trial. After a careful evaluation of the problematic of germination it was decided to order a new dose of seeds from the same company and add to all the pots the same number of seeds as was done at the beginning. Although the new dose seemed to grow better, most of the individuals did not meet the grow level of the other species. *Prunella* probably did not manage to succeed in the competition with earlier germinated species. However, the reason of the original problem is unknown. It could be caused by competition for light, water or nutrient with the other species.

Table II.: Characteristics of the gardening substrate used.

mixture of little to moderate and severe decomposed peat (H2 - H8), green waste compost, bark humus and clay		
humidity max. 65%		
combustibles in dry matter min. 25%		
pH (CaCl2) 5 - 6.5		
electrical conductivity (in aqueous extract 1:25) max. 1.2 mS/cm		
content of particles bigger than 20 mm max. 5%		
salinity (KCl) < 3.0 g/l		
available nutrients:	N 70 - 300 mg/l	
	P2O5 min. 80 - 500 mg/l	
	K2O min. 100 - 1200 mg/l	
content of elements of risk (mg/kg) : As 10, Cd 1, Cr 100, Cu 100, Hg 1.0, Mo 5, Ni 50, Pb 100, Zn 300		

2.2. Data collection

After three months in the common garden, with periodic watering, grown plants were harvested in the second half of July (21st-31st July) for following traits to be measured: aboveground biomass and plant height as functional traits related to competitive strength and plant fertility, specific leaf area (SLA), which reflects growth and photosynthetic rate of leaf and usually exhibits higher values in resource-rich environments, and leaf dry matter content (LDMC), which is a trait demonstrating leaf density connected with the ability of nutrient utilization (Knevel *et al.*, 2005). Unfortunately due to quite a big extent of the experiment not all the pots could be included. Therefore, two randomly chosen replicates of all the mixtures and four replicates of the monocultures with densities proportional to the mixtures (60 individuals) were used. For the trait measuring five individuals of each species in the pot were randomly chosen and processed.

First, in each pot five whole individuals (tufts including old dead biomass) were chosen randomly for later measurements. Then the total pot biomass was cut and sorted out according to the species. All the plants were cut right above the ground. On the chosen individuals, the height was measured with an accuracy of millimeters as the height of the highest stem in the tuft or the height of the blooming stem (only occurred with *Achillea*). Then, several leaves were cut off (number depending on their size), weighed on an analytical balance with an accuracy of 10^{-4} g and scanned with a resolution of 300 dpi to get values necessary for computing SLA and LDMC. Scans were adjusted in Photoshop and processed by a R script to compute their leaf area (LA) values. The results were compared with LA values computed in Photoshop and considered meaningful as the mean absolute difference was not bigger than expected (2.6 %). The total biomass (sorted out according to the species), cut off leaves and rests of the individuals the leaves were isolated from were dried in a drying machine at 80ºC for 48 hours. Immediately before weighing the dry biomass, each dose was dried again at 80ºC for 3 more hours. Posteriorly, it was weighed on analytical balance with an accuracy of 10^{-4} g when lighter than 0.5 g or on a balance with an accuracy of 10^{-2} g when heavier than 0.5 g. SLA was then computed as the LA value (mm^2) divided by the weight of the dry leaf biomass (mg). LDMC responds to the ratio of the weight of the dry leaf biomass (mg) to the weight of the fresh leaf biomass (g). Finally, all the trait values were log-transformed due to great differences among traits of different species. These log-transformed data were used for computing variances and mean values of all measured traits for each quintuplet of representative individuals of each species in all pots

as well as for computing biodiversity effects and within-species, between-species and total community variances in the pot communities (see next section).

2.3. Data processing

The mechanism by which diversity directly influences community functioning is called net biodiversity effect (see introduction). This is composed of two processes operating in combination, the complementarity effect arising from niche differentiation and facilitation between species, and the selection effect based on dominance of species with particular traits (Loreau and Hector, 2001). To disentangle these two mechanisms, the method of additive partitioning by Loreau and Hector (2001) was used. The net biodiversity effect, the complementarity effect and the selection effect were computed for each pot according to the following formula (Equation 1).

$$\Delta Y = N\overline{\Delta RY}\,\overline{M} + Ncov(\Delta RY, M)$$

<div align="right">Equation 1</div>

In this equation ΔY represents the net effect as a sum of complementarity effect, $N\overline{\Delta RY}\,\overline{M}$, and selection effect, $Ncov(\Delta RY, M)$. The individual constituents mean: ΔY – deviation from total expected yield of the mixture, N – number of species in the mixture, ΔRY - deviation from expected relative yield of species i ($\overline{\Delta RY}$ meaning the average), M - monoculture yield of species i ($\overline{M}$ meaning the average).

This approach, i.e. decomposition of net effects components, was used to assess possible changes in trait values and variability of individual species in response to biodiversity effects operating in the community and compare them with their response to species richness. Statistica 12.0 was used to express the dependence of mean trait values and variances, both computed from log-transformed data, on species richness, net biodiversity effect, complementarity effect and selection effect, respectively, by a simple regression. The significant results are represented by the coefficient of determination (R^2) demonstrating the proportion of total variation of outcomes explained by the regression model and by the sign of the regression coefficient determining the direction of the dependence (Table III.).

The evaluation of the community functioning on the level of pots was the other important aspect of this experiment. It builds on the idea of partitioning the total functional

diversity into between-species functional diversity being reflective of trait dissimilarities in a community because of differences among species and within-species functional diversity reflecting trait dissimilarities in a community caused by intraspecific variability (de Bello *et al.,* 2011). The method of the total variance decomposition first formalized by de Bello *et al.* (2011) was used to compute the following quantities: community weighed mean of particular trait of all individuals in the community, between-species variance, within-species variance and total variance as a sum of the two previous. The left side of the Equation 2 represents the total community trait variance; the right side corresponds to the between-species variance and within-species variance, respectively. The community weighed mean is represented by the figure x_{com} (de Bello *et al.,* 2011).

$$\sum_{i=1}^{Nsp} \frac{1}{Nsp} \sum_{a_i=1}^{Nind_i} \frac{1}{Nind_i} (x_{ai} - x_{com})^2$$

$$= \sum_{i=1}^{Nsp} \frac{1}{Nsp} (x_i - x_{com})^2 + \sum_{i=1}^{Nsp} \frac{1}{Nsp} \sum_{a_i=1}^{Nind_i} \frac{1}{Nind_i} (x_{ai} - x_i)^2$$

Nsp – number of species in the community

Nind_i – number of individuals measured within each species

x_{ai} – trait value of individual *a* of species *i*

$x_i = \sum_{a_i=1}^{Nind_i} \frac{1}{Nind_i} x_{ai}$ - average trait value of species *i*

$x_{com} = \sum_{i=1}^{Nsp} \frac{1}{Nsp} x_i$ - average trait value across all species in the community

Equation 2

To compare the results obtained in this study to those of Violle *et al.* (2012) $T_{IP/IC}$ was counted as the ratio of within-species variance to the total community variance. Values of community weighed mean, between-species variance, within-species variance, total community variance and $T_{IP/IC}$ of all traits in all pots were put in a linear regression with the number of species in the pot community and with all measured biodiversity effects. The results of the dependence of these quantities on species richness and the biodiversity effects are demonstrated by the R^2 value and the sign of the regression coefficient in Table IV.

3. Results

3.1. Relationship between functional traits of individual species, species richness and related biodiversity effects

Mean trait values and variances of trait values of individual species, from log-transformed data, were put in a linear regression as a variable dependent on species richness, net biodiversity effect, complementarity effect and selection effect respectively. The results represented by the R^2 value and the sign (+/-) of the regression are summarized in the Table III. The most significant relationships were found between mean trait values of height, biomass and species richness (see Figure 1 and 2) and the net biodiversity effect (see Figure 3 and 4). These two out of four traits measured showed significantly negative dependence of mean trait values on the number of species for all six species with R^2 values ranging from 0.08 at competitively strong *Holcus* to 0.40 at *Prunella*, competitively weak. As such, the results showed stronger patterns for less competitive species. The relationship of the same mean trait values and the net biodiversity effect developed significantly positive at four species (*Achillea, Agrostis, Holcus, Lychnis*) in both cases. It means the opposite reaction of species functional traits on the number of species and on the net biodiversity effect. This tendency can be partly explained by the shape of the net effect dependence on species richness. It decreased with the number of species and exhibited substantially positive values only for the two, three and four species mixtures, remaining below zero in high diversity communities (see Figure 5). Furthermore the complementarity effect and the selection effect showed mostly positive relationship with mean values of functional traits, though not significant so frequently. Again, there can be observed decreasing values of both complementarity and selection effects with increasing species richness of a community, however, this time the range of the values narrows from both plus and minus side towards zero more equally (see Figure 6 and 7). The only case of positive correlation of influences of the number of species, net effect and complementarity effect on mean trait value was found at specific leaf area of *Festuca*.

Within species, no significant trend of trait variance in response to the number of species or the biodiversity effects was found. Nevertheless, some response of within-species variance to species diversity was found on the level of whole pot communities (see next section).

Table III.: Summary of dependence of mean and variance in trait values within single species on the number of species in the pot (NSP), net biodiversity effect (NE), complementarity effect (CE) and selection effect (SE) expressed as R^2 value and a sign of the regression. Values in bold respond to significant values ($p < 0.05$), common print represents values nearly significant ($0.1 > p < 0.05$) and 'ns' deputizes for not significant results.

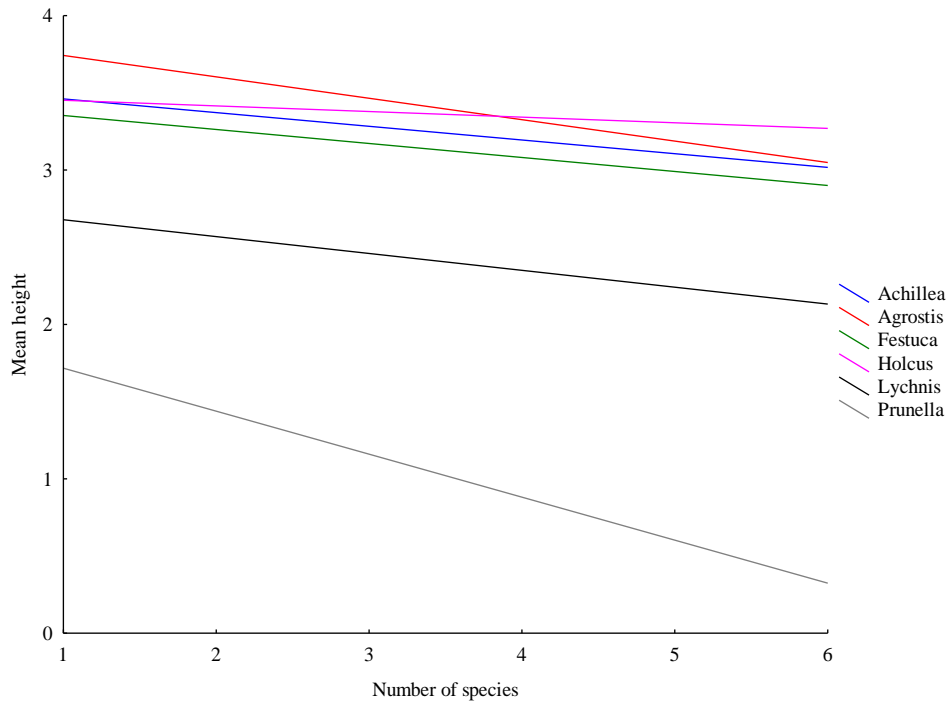|	Height							
	Mean				**Variance**			
	NSP	**NE**	**CE**	**SE**	**NSP**	**NE**	**CE**	**SE**
Achillea	**0.10** (-)	**0.24** (+)	**0.19** (+)	**0.08** (+)	ns	ns	ns	ns
Agrostis	**0.33** (-)	**0.21** (+)	**0.12** (+)	**0.10** (+)	ns	ns	ns	0.03 (+)
Festuca	**0.32** (-)	ns	ns	**0.08** (+)	ns	0.05 (-)	ns	0.04 (-)
Holcus	**0.08** (-)	**0.29** (+)	**0.29** (+)	ns	0.04 (+)	0.04 (-)	ns	ns
Lychnis	**0.33** (-)	**0.32** (+)	**0.18** (+)	**0.06** (+)	**0.09** (+)	**0.10** (-)	**0.08** (-)	ns
Prunella	**0.40** (-)	ns	ns	ns	0.04 (+)	ns	ns	ns
	Biomass							
	Mean				**Variance**			
	NSP	**NE**	**CE**	**SE**	**NSP**	**NE**	**CE**	**SE**
Achillea	**0.18** (-)	**0.18** (+)	**0.18** (+)	ns	ns	ns	ns	**0.07** (+)
Agrostis	**0.33** (-)	**0.08** (+)	ns	**0.10** (+)	ns	**0.06** (+)	ns	0.05 (+)
Festuca	**0.49** (-)	ns	0.04 (-)	**0.09** (+)	**0.06** (+)	ns	ns	ns
Holcus	**0.08** (-)	**0.18** (+)	**0.21** (+)	ns	ns	ns	ns	ns
Lychnis	**0.19** (-)	**0.10** (+)	ns	**0.08** (+)	ns	ns	0.04 (-)	ns
Prunella	**0.40** (-)	ns	ns	ns	ns	ns	ns	0.05 (-)
	Specific leaf area							
	Mean				**Variance**			
	NSP	**NE**	**CE**	**SE**	**NSP**	**NE**	**CE**	**SE**
Achillea	ns	ns	ns	ns	ns	ns	ns	ns
Agrostis	ns	0.04 (+)	ns	ns	ns	ns	ns	ns
Festuca	**0.10** (+)	**0.17** (+)	**0.14** (+)	ns	ns	ns	ns	ns
Holcus	ns	**0.11** (+)	**0.10** (+)	ns	ns	ns	ns	ns
Lychnis	0.04 (+)	ns	**0.07** (+)	**0.17** (-)	0.04 (-)	**0.07** (+)	ns	**0.14** (+)
Prunella	ns	ns	ns	0.05 (+)	ns	ns	ns	ns
	Leaf dry matter content							
	Mean				**Variance**			
	NSP	**NE**	**CE**	**SE**	**NSP**	**NE**	**CE**	**SE**
Achillea	ns	ns	ns	ns	ns	ns	ns	ns
Agrostis	ns	ns	ns	ns	ns	ns	ns	ns
Festuca	ns	ns	ns	ns	ns	ns	ns	ns
Holcus	ns	ns	ns	ns	ns	ns	ns	ns
Lychnis	ns	ns	**0.12** (-)	**0.15** (+)	ns	ns	ns	ns
Prunella	ns	**0.10** (+)	**0.06** (+)	**0.08** (+)	**0.09** (+)	**0.06** (-)	**0.07** (-)	ns

Figure 1: Mean values of height (computed from log-transformed data expressed in cm) exhibited a significantly negative relationship with species richness for all six species included in the experiment. *Prunella* showed to be the weakest and *Holcus* the strongest competitor regarding the plant height.
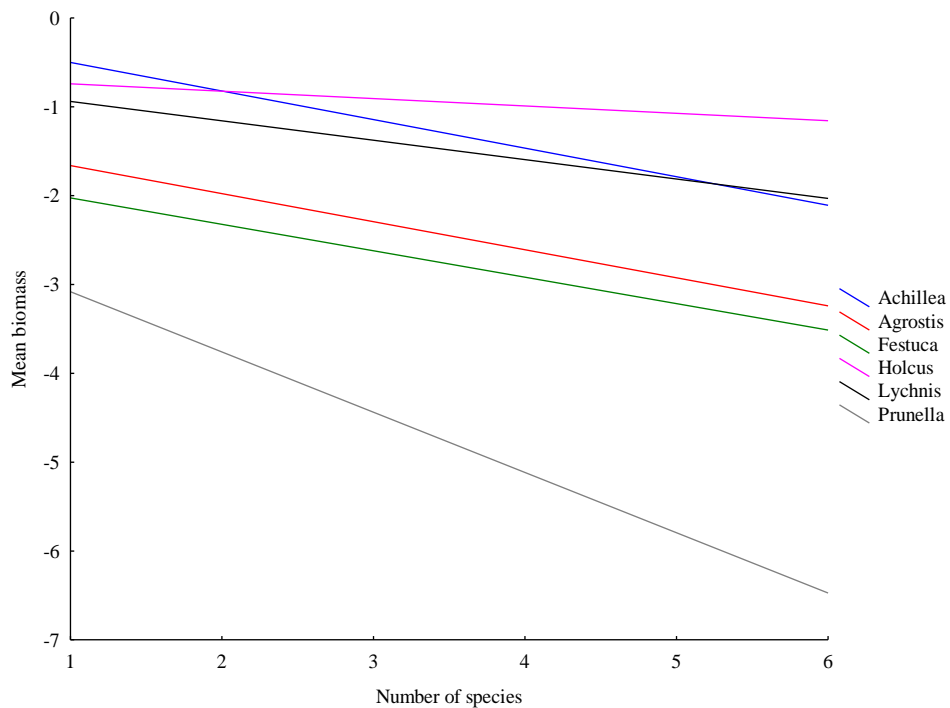

Figure 2: Mean values of biomass (computed from log-transformed data expressed in g) exhibited a significantly negative relationship with species richness for all six species included in the experiment. *Prunella* showed to be the weakest and *Holcus* the strongest competitor regarding the plant biomass.
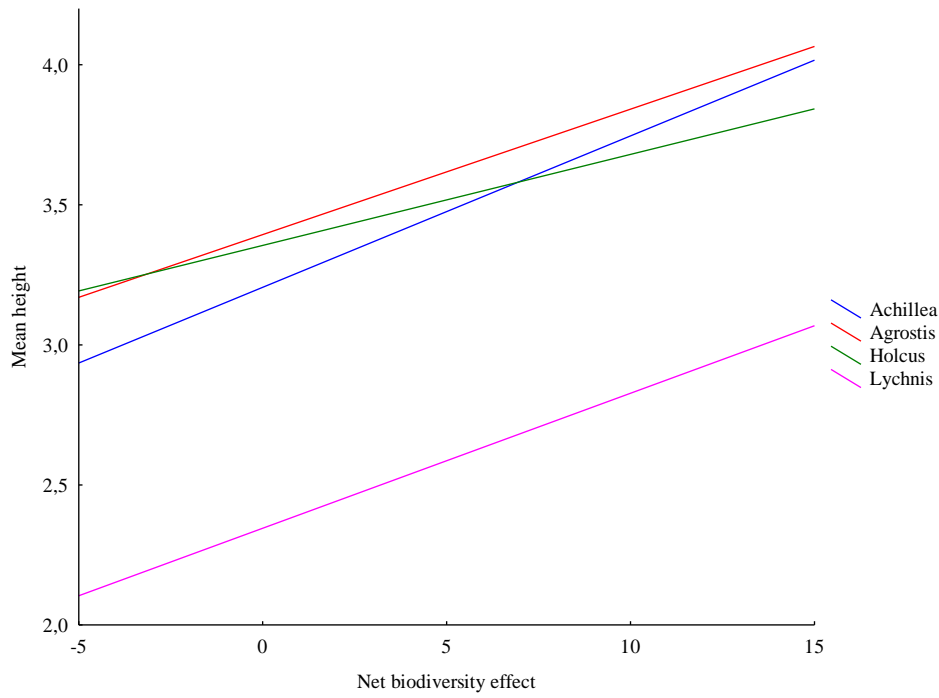
Figure 3: Mean height values of four our out of six species in the experiment exhibited significantly positive relationship with the net biodiversity effect. The relationship for *Prunella* and *Festuca* was not significant.
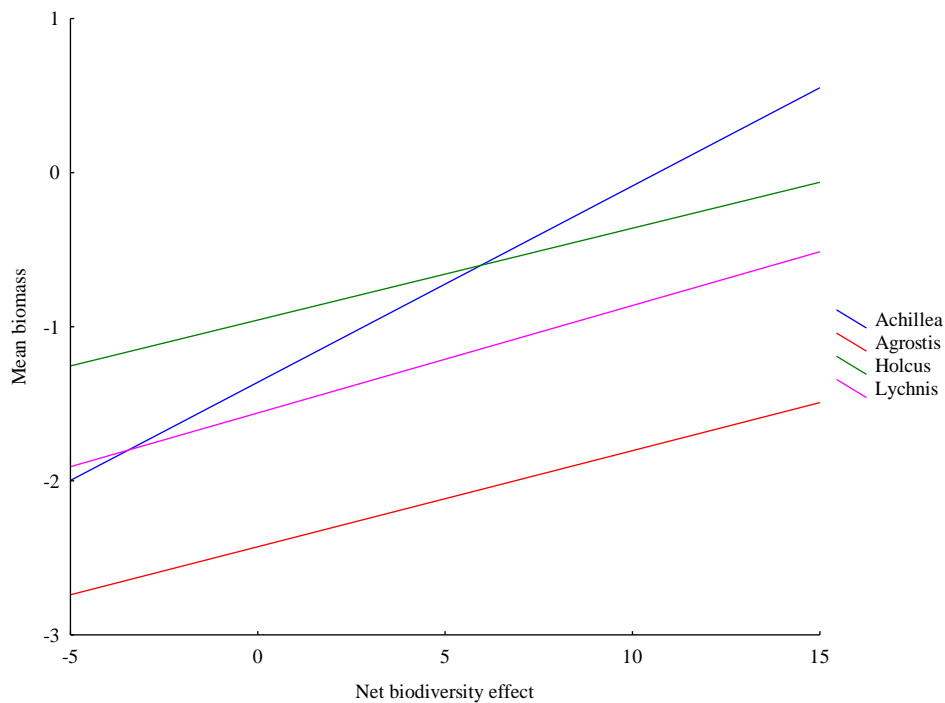

Figure 4: Mean biomass values of four our out of six species in the experiment exhibited significantly positive relationship with the net biodiversity effect. The relationship for *Prunella* and *Festuca* was not significant.
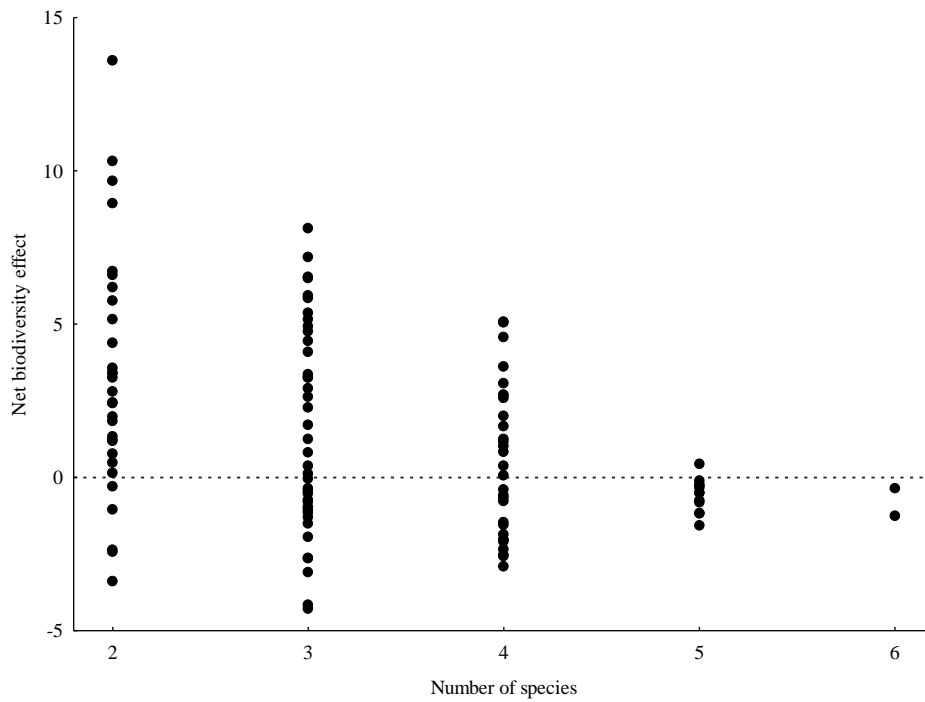
Figure 5: Net biodiversity effect decreased with increasing number of species in the community. Substantial part of net effect values was found below zero on all diversity levels, however, in highly diverse communities (5 and 6 species) the minus values prevailed.
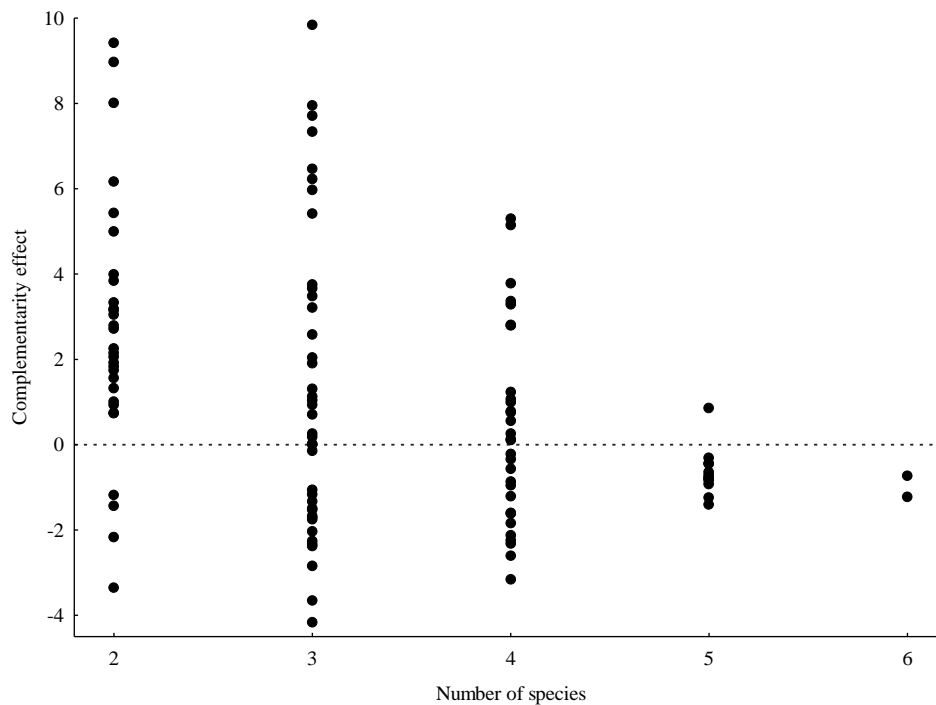

Figure 6: Positive complementarity effect predominated in communities composed of low number of species (2, 3), at the diversity level 4 the plus and minus values were almost equally represented while in more diverse communities (5, 6) negative complementarity effect prevailed.
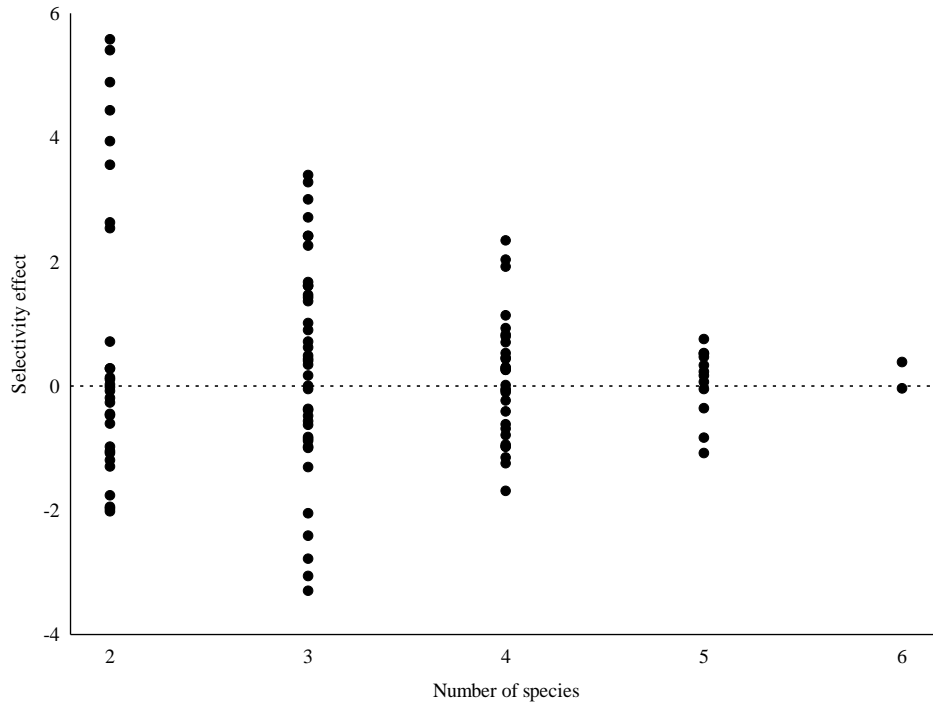
Figure 7: Positive and negative values of selection effect were nearly equally represented across all species richness levels with the range of the values gradually decreasing with increasing number of species in the community.

3.2. Relationship between functional diversity components, species richness and biodiversity effects in pot communities

Log-transformed data were used to compute community weighed mean, functional diversity components (between-species variance, within-species variance and total community variance) and $T_{IP/IC}$ for the four traits measured in the pot communities. These quantities were included in a linear regression as variables dependent on species richness, net biodiversity effect, complementarity effect and selection effect respectively. The results represented by the R^2 value and the sign (+/-) of the regression are summarized in the Table IV. The most important findings were expected at the relationship between within-species variance, between-species variance and species richness. Significant response of within-species variance to the number of species was only found at biomass, where the relationship was negative with R^2 0.04 (see Figure 8). The relationship of between-species variance and the number of species was more pronounced. It increased at three traits including height, biomass and specific leaf area with R^2 value about 0.10 indicating some amount of niche partitioning (Fig. 9). Reaction of within- and between-species variance on increasing influence of biodiversity effects was opposite to the reaction on the number of species.

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Within-species variance of specific leaf area responded positively to the net biodiversity effect while between-species variance responded negatively. Within species variances of both biomass and specific leaf area were influenced positively by increasing selection effect whereas between-species variance of the same traits showed negative relationship with the selection effect. The total community variance was positively influenced by the selection effect at height, biomass and specific leaf area. These reactions of trait variances on the selection effect may indicate lowered ability of interspecific variability among suppressed species, while the species dominating the community had to increase its intraspecific variability to cope with the strong intraspecific competition.

Another significant dependence was found between $T_{IP/IC}$ of height, biomass and specific leaf area and the number of species. $T_{IP/IC}$ decreased with R^2 about 0.10 in response to the increasing species richness, indicating narrowing of niche widths of individual species with the presence of more competitors in the community (Figure 10). This kind of relationship between $T_{IP/IC}$ and species richness implies support of the niche theory. $T_{IP/IC}$ also exhibited positive response to the net biodiversity effect and the selection effect at three traits including biomass, specific leaf area and leaf dry matter content.

Community weighed mean behaved predictably in the case of biomass, where positive correlation with the number of species and negative correlation with the biodiversity effects could be expected from the behaviour of mean biomass values of individual species in response to these quantities. Different relationship occurred at specific leaf area, where the community weighed mean responded positively to both number of species and complementarity effect while its reaction to increasing selection effect was negative. Some differences at the trait of specific leaf area were already implied on the level of species, where *Festuca* showed positive correlation between reactions to the number of species and the net effect, unusual in cases of other traits. On the contrary, leaf dry matter content correlated the community weighed mean with both the net effect and the complementarity effect negatively.

Table IV.: Summary of dependence of community weighed mean (CWM), within-species variance (WVar), between-species variance (BVar) and total community variance (TotVar) in a pot on the number of species in the pot (NSP), net biodiversity effect (NE), complementarity effect (CE) and selection effect (SE) expressed as R^2 value and a sign of the regression. Figures in bold respond to significant values ($p<0.05$), common print represents values nearly significant ($0.1>p<0.05$) and 'ns' deputizes for not significant results.

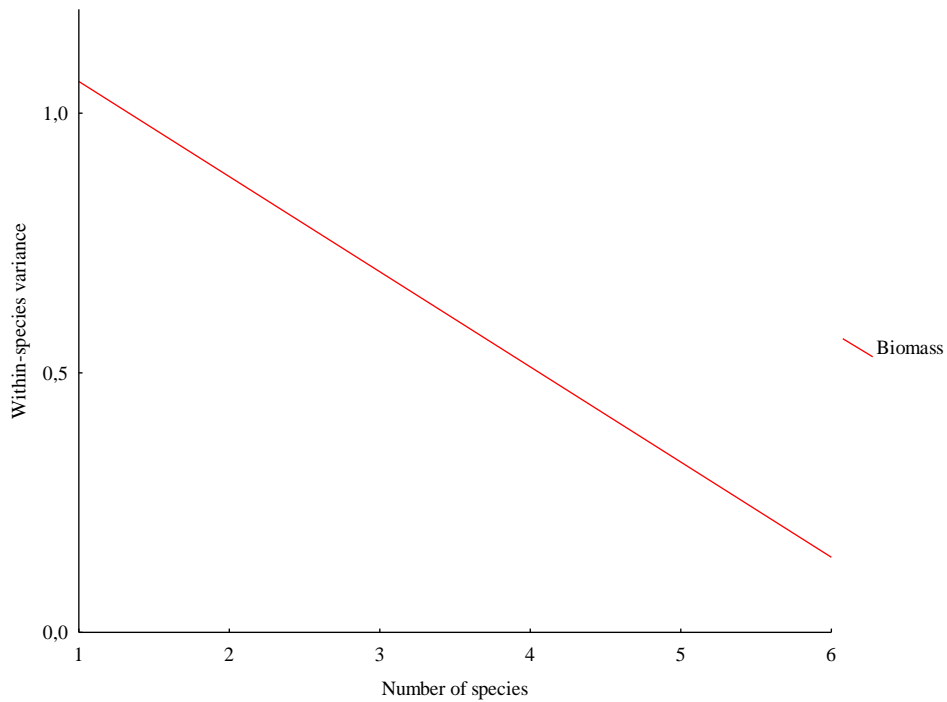|	Height				
	CWM	WVar	BVar	TotVar	$T_{IP/IC}$
NSP	ns	ns	**0.10 (+)**	**0.06 (+)**	**0.07 (-)**
NE	ns	ns	ns	ns	ns
CE	ns	ns	ns	ns	ns
SE	ns	ns	ns	**0.07 (+)**	ns
	Biomass				
	CWM	WVar	BVar	TotVar	$T_{IP/IC}$
NSP	**0.05 (-)**	**0.04 (-)**	**0.13 (+)**	ns	**0.09 (-)**
NE	**0.12 (+)**	ns	ns	**0.08 (+)**	**0.06 (+)**
CE	**0.14 (+)**	ns	ns	ns	ns
SE	ns	**0.03 (+)**	**0.08 (-)**	**0.09 (+)**	**0.19 (+)**
	Specific leaf area				
	CWM	WVar	BVar	TotVar	$T_{IP/IC}$
NSP	**0.04 (+)**	ns	**0.08 (+)**	ns	**0.10 (-)**
NE	ns	**0.03 (+)**	**0.12 (-)**	ns	**0.13 (+)**
CE	**0.03 (+)**	ns	**0.05 (-)**	ns	0.02 (+)
SE	**0.02 (-)**	**0.08 (+)**	**0.08 (-)**	**0.05 (+)**	**0.18 (+)**
	Leaf dry matter content				
	CWM	WVar	BVar	TotVar	$T_{IP/IC}$
NSP	ns	ns	ns	ns	ns
NE	**0.09 (-)**	ns	ns	ns	0.03 (+)
CE	**0.09 (-)**	ns	ns	ns	ns
SE	ns	ns	ns	ns	**0.15 (+)**

Figure 8: Within-species variance in biomass values decreased in the pot communities from the highest values in monocultures to the lowest in six species mixtures. The line shows the predicted values according to the models described in Table IV.
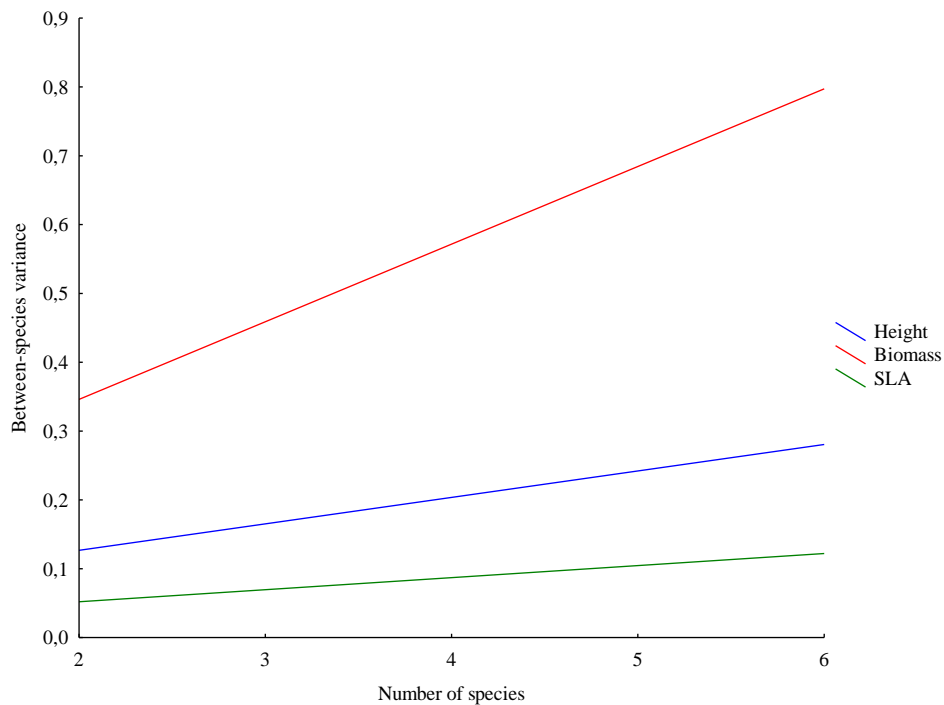

Figure 9: Between-species variance in height, biomass and specific leaf area (SLA) increased with the number of species in pot communities. The most significant influence was observed on biomass. The lines show the predicted values according to the models described in Table IV.
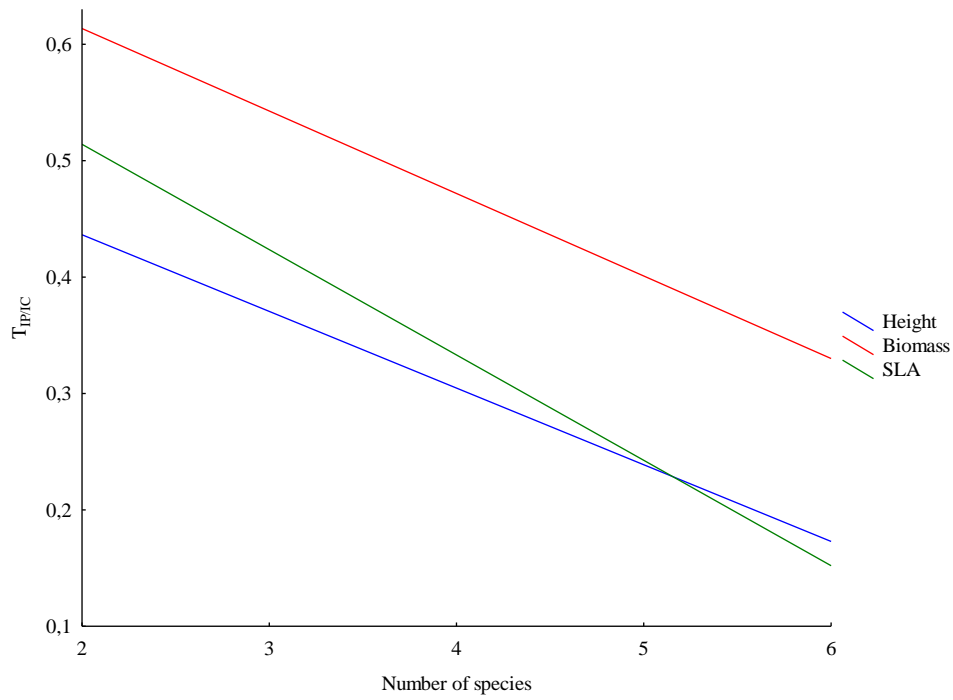
Figure 10: Negative relationship between $T_{IP/IC}$ (within-species variance relative to the total variance of the community) and the number of species was found for height, biomass and specific leaf area (SLA). Increase of species richness means reduction of local intraspecific variation of these traits. The lines show the predicted values according to the models described in Table IV.

4. Discussion

In order to explore intraspecific variability of functional traits in communities of variable species diversities, an experiment was designed based on previous theoretical frameworks (e.g. Violle *et al.,* 2012). Results of this experiment were evaluated with regard to the two objectives of the thesis: 1) to investigate the response of functional traits and their variability to species richness and biodiversity effects (net effect, complementarity effect and selection effect) at the level of individual species, 2) to explore the importance of intraspecific trait variability in whole pot communities and its trends in relation to changing species richness and corresponding biodiversity effects.

The first question taken into account while interpreting the results was the level of species. Mean in trait values within species changed much more than variance along the species richness gradient. With the number of species representing the predictor variable mean height and biomass showed negative correlation for all six species. In general, most changes in mean trait values were found with species richness particularly for species that are less dominant and competitive, suggesting that these species vary more in their traits along gradients of biotic interactions. In cases of both mean height and biomass the dependence was most significant for *Prunella*, which showed to be a weak competitor suppressed in all the mixtures, partly due to its late germination, partly due to its short procumbent stems.

By contrast, the smallest slope of the regression line belonged to *Holcus*, which appeared to be the most successful species across all diversities and species combinations and it is generally a competitive species. Nevertheless, according to the results the competitive success of *Holcus* does not seem to be achieved by changing greatly trait values as the relationship of its mean trait values and the selection effect is insignificant in all cases. *Holcus lanatus* appears, on the contrary, to be favored thanks to good use of the complementarity effect. In spite of its competitive ability not even *Holcus* showed higher growth rates in the mixtures than in the monocultures, indicating that its intraspecific competition was not stronger than interspecific competition in the mixtures as it was implied in previous studies of dominant species (Roscher *et al.,* 2005).

When the net effect was considered to be the predictor variable, four of the six species included showed significantly positive correlation for both mean height and biomass. The relationship of *Prunella* and *Festuca* and the net biodiversity effect was not significant.

In most of the significant relationships the positive correlation of mean trait values and the net effect was based on the complementarity between species rather than on the selection effect.

The opposite character of the relationship between mean trait values of height and biomass and the number of species versus the net effect can appear strange on the first sight. However, the importance of the net biodiversity effect in this experiment decreases with increasing species richness. A similar tendency was found for both complementarity effect peaking in the mixtures of 2 and 3 species and then decreasing and for the selection effect decreasing more or less gradually across all the richness levels. This shape of the relationship of biodiversity effects and species richness is in contradiction with findings of Roscher *et al.* (2005) established as a part of the 'The Jena Experiment'. A curvilinear dependence of the complementarity effect on species richness peaking at low species levels and a linear relationship of the selection effect increasing with increasing number of species was found by Roscher *et al.* (2005). It is necessary to mention that Roscher *et al.* (2005) operated with much wider range of species than this experiment discussed. An increase of species pool of this experiment may change the relationships of biodiversity effects and species richness for example if more dominant species were included. Also it should be noted that in our experiment we excluded species with strong height differences, contrary to Roscher *et al.* (2005).

At the community level, the main goal was to test the changes of within- and between-species variance and the ratio of within-species variance relative to the total variance of the community ($T_{IP/IC}$) in response to increasing species richness and to relate them to the hypothesis suggested in the study by Violle *et al.* (2012). The only trait which exhibited significant response of within-species variance to species richness was the biomass showing negative correlation. This negative relationship means a reduction of niche widths of individual species with increasing number of species in the community and opposes the idea of 'individual variation' theories that the intraspecific variation could be the main driver of diversity in this experiment. This finding markedly contrasts to the results of the study by La-Bagousse-Pinguet *et al.* (2014), which revealed the within-species variance for height and its positive relationship with species richness to be the main component of functional diversity related to species richness.

Between-species variance and its relationship with the number of species brought more significant results to this research. Three functional traits showed positive correlation between interspecific variance in the communities and their species richness. In terms of niche partitioning it indicates increased mean trait differences with increasing number of species. In other words, in species-rich communities species have to increase trait distance among different populations possibly to reduce interspecific competition and be able to coexist. In fact, from the behaviour of within- and between-species variance in response to species richness the course of the correlation between $T_{IP/IC}$ and the number of species in the community can be already predicted, supporting the view that species overlap lessens with increasing species richness, which matches the niche theory (Violle *et al.,* 2012).

The intraspecific variability representing the numerator in the formula decreases and so its ratio in the total community variance influenced by increasing interspecific variance must clearly decrease. The negative correlation of $T_{IP/IC}$ and species richness was confirmed by three significant results of a simple regression for height, biomass and specific leaf area. Fig. 10 displays the relationship as a dependence of $T_{IP/IC}$ ratio on the number of species while Violle *et al.* (2012) presents it reversely, as a dependence of species richness on $T_{IP/IC}$. In fact, the orientation of the axis is of a minor importance as $T_{IP/IC}$ and species richness show a correlative relationship, where it is not clear which variable is the predictor and which the dependent one. The shape of the reached relationship between $T_{IP/IC}$ and species richness also found no support in Bagousse-Pinguet *et al.* (2014)'s study where these two quantities were found to correlate positively suggesting an increase in niche overlap in highly diverse communities and partly relating its results to the 'individual variation' theories. However, the low number of significant results for intraspecific variability in this experiment discussed may be considered with caution.

The reason of low significance of intraspecific variability may be due to the origin of the seed pool (supplied by only one company) resulting in poor seed genetic variation, but at least it was the same in all pots (thus limiting the effect of different populations, therefore genetic effects, instead of plasticity). Hence, low intraspecific variability still represents little trait plasticity in response to biotic interactions but we cannot exclude that in a more genetically different population selection of different genotypes would follow. This component deserves attention in future experiments.

In the experiment carried out in this thesis, the down slope of the line relating $T_{IP/IC}$ to species richness corresponds with the graph suggested by Violle *et al.* (2012) for the classic niche-theory. Therefore, results of this thesis support the idea of niche partitioning among species in the community, when increasing number of competitors causes thinning of the range of resources available for one species in the community and narrowing of species niches accompanied by reduced intraspecific diversity.

5. Conclusions

This thesis aimed to evaluate the importance of intraspecific variability in plant communities of different species diversity and intensity of biodiversity effects operating in the species mixtures. On the basis of previous studies on this topic a pot experiment in a glasshouse was designed and six plant species included: *Lychnis flos-cuculi, Achillea millefolium, Prunella vulgaris*, *Agrostis tenuis, Holcus lanatus* and *Festuca rubra.* Using a pot experiment allow to control for factors which are not easy to control using field experiments. A set of results on species traits values (biomass, plant height, SLA, LDMC), trait variances (within-species, between-species, total community variance) and biodiversity effects (net biodiversity effect, complementarity effect, selection effect) were obtained and included in linear regressions considering two functional levels, level of species and level of whole communities. As a summary of the study, the following main conclusions can be drawn:

1) Mean trait values of biomass and height showed positive correlation with species richness for all six species considered, indicating all species to prosper worse in presence of interspecific competition.

2) The importance of the net biodiversity effect decreased with increasing species richness resulting in unexpectedly negative response of mean trait values (biomass and height) to the net effect.

3) The tendency of within-species variance to change with increasing number of species in the community was significant only at the community level for biomass, which exhibited negative correlation. This kind of relationship suggests reduction of niche widths with increasing species richness and opposes the 'individual variation' and 'neutral' theories.

4) More proposed results were obtained for between-species variance in reponse to species richness. Positive correlation was found for three traits (biomass, height, SLA) suggesting trait distance between species to increase with strengthening interspecific competition.

5) The proportion of the intraspecific variance in the total community variance ($T_{IP/IC}$) vas related to species richness negatively. On the basis of this relationship present thesis supports the idea of niche-based ecological theory.

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