

University of Tartu  
Faculty of Science and Technology  
Institute of Ecology and Earth Sciences  
Department of Botany

Hanna Kaarin Hermlin

**The role of morphological plasticity in plant  
species  
coexistence**

Ecology and Biodiversity Conservation

Master's thesis (30 EAP)

Supervisor: professor Kristjan Zobel

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## **Morfoloogilise plastilisuse roll taimede koeksisteerimisel**

Taimed on sessiilsed organismid, mistõttu peavad nad edu saavutamiseks ümbritseva keskkonnaga kohanema. Pidevalt muutuvad valgustingimused, ebaühtlaselt jaotunud toitained, alalõpmata muutuv vee kättesaadavus ning teiste taimedega konkureerimine on vaid mõned taimede käekäiku mõjutavad tegurid. Üks mehhanism keskkonnamuutustega kaasaminemiseks on morfoloogiline plastilisus – omadus kujundada käesolevale keskkonnale sobivaim morfotüüp ehk väliskuju. Näiteks pikendavad varjutatud taimed oma varsi ja leherootse, piiravad harunemist ning suurendavad lehe eripinda, kõik selleks, et varjust valgusesse püüelda. Morfoloogiline plastilisus tekitab suure liigisisese taimeomaduste varieeruvuse, mil on viimasel ajal tõestatud olevat oluline taimekooslusi mõjutav efekt. Veelgi enam, morfoloogilisel plastilisusel on leitud ka otsene liigirikkust edendav mõju. Seetõttu püstitasin selles töös hüpoteesi „Plastilisus edendab taimeliikide koeksisteerimist“ ning viisin läbi potikatse, kus iga pott sisaldab neljaliigilist kooslust, iga kooslus eri määral plastiline. Üleskasvanud koosluse taksonoomilise mitmekesisuse hindamiseks mõõtsin lisaks teistele parameetritele iga poti jaoks koos kasvavate liikide ohtruse ühtluse, kasutades ohtruse hindamiseks paralleelselt nii liigi katteväärtust kui maapealset biomassi.

Tööhüpoteesi kontrollimisel ilmnid vastandlikud tulemused. Hüpotees vastas tõele, kui vaatluse all olid lehtede arvu ja lehepikkuse plastilisuse indeksid, lisaks ka lehepindala ja lehtede arvu kombineeritud plastilisuse indeks – koosluse suur keskmine plastilisus ennustas suuremat ühtlust. Huvitaval kombel leidsin hoopis vastupidise tulemuse juhul kui vaatluse all oli keskmine lehe eripinna plastilisus. Juhul kui kokku olid juhtunud lehe eripinna poolest plastilised liigid, kujunes(id) koosluses välja selge dominant (dominandid) ja diversiteet jäi madalaks.

Tulemused kinnitavad, et taimede morfoloogiline plastilisus mängib koosluste dünaamikas olulist rolli, kuid erinevate mõjude ja mehhanismide rohkuse tõttu on keeruline ennustada, kas plastilisuse mõju on kokkuvõttes taimede kooselu soodustav või takistav.

Märksõnad: taimede morfoloogiline plastilisus, liikide koeksisteerimine, ühtlus, konkurents, koeksisteerimise mehhanismid.

CERCS kood: B270- Taimeökoloogia

## **The role of morphological plasticity in plant species coexistence**

As plants are sessile organisms, their key to ecological success is to adapt with changing environmental conditions such as light availability, nutrient status, water supply or competitive stress from neighbouring plants. One of the key mechanisms to achieving that is morphological plasticity – the inherent ability to always express the morphotype currently most suitable to match the ever-changing environment. For example, when shaded, plants increase the length of stems and petioles, reduce branching and increase their specific leaf area, all to escape the shadow and pursue light. Morphological plasticity cultivates great intraspecific trait variability, recently proved as an important factor affecting plant community composition. Moreover, plasticity has been found to directly promote species coexistence. Therefore, I posed an hypothesis “Plasticity promotes species coexistence” and conducted an outdoor pot experiment, where each pot contains a four species community, each community different in its mean plasticity. To assess the taxonomic diversity of a full-grown community, besides other parameters, I measured the evenness of abundance of the species within a pot, using each species coverage and above-ground biomass as the measure of abundance.

Testing the hypothesis revealed inconclusive results. The hypothesis was confirmed when plasticity in leaf number and leaf length, as well as a combined plasticity index of leaf area and leaf number was under observation – greater community mean plasticity predicted greater evenness of abundance. Surprisingly, I found an opposite result when plasticity in specific leaf area was under observation. When species with high plasticity in specific leaf area happened to grow beside one another, definite dominant(s) stood out and community diversity was low.

Results imply that morphological plasticity has an effect on plant community dynamics, but because of the complexity of the nature of its effects, there is no definitive answer whether plasticity promotes or hinders species diversity.

Keywords: plant morphological plasticity, species diversity, species coexistence, evenness, competition, coexistence mechanisms.

CERCS Code: B270- Plant ecology

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# INTRODUCTION

## 1. Plant morphological plasticity

Phenotypic plasticity can be defined as the ability to ontogenetically adapt with changing environment such as changing light conditions, unevenly scattered soil nutrients or the availability of water, caused by both biotic and abiotic factors. In plants, phenotypic plasticity can frequently be observed in shoot morphology. Morphological plasticity incorporates environment-induced changes in mean leaf area (Weijschedé *et al.* 2006), petiole length (Weijschedé *et al.* 2006, Millenaar *et al.* 2005) or branching. For example, when shaded by neighbours, soybean (*Glycine max*) activates its shade avoidance response, reducing branching and increasing internode elongation (Green-Tracewicz *et al.* 2011). Some plants are also able to adjust their allometric trajectory to current environmental status. Because of limited resource supply, photosynthates allocated to one function or organ are mostly not available to others. Since it is more reasonable to allocate resources to enhance the uptake of the limiting resource, shaded plants are expected to increase their above-ground biomass at the expense of below-ground biomass. This leads to a decreasing root:shoot biomass ratio (Weiner 2004). At the same time, it must be acknowledged that pure allometric growth, without radical changes in allometric trajectory, is considered “apparent plasticity”, as all plants concentrate their growth on specific organs during different growing stages. For example, at the beginning of the growing season, *Senecio vulgaris* allocates most of its biomass to roots, whereas allocation to seeds reaches its maximum at the end of its life cycle (Harper and Ogden 1970). True plastic responses can be differentiated into two groups according to their complexity: modular plastic responses and integrated plastic responses. Modular plastic responses lead to local proliferation in resourceful patches and various local physiological responses as the differentiated growth of sun and shade leaves. The more complex, integrated responses incorporate changes in allometric trajectory or integrated physiological differentiation such as induced defences which both require a degree of communication among the parts of a plant (Weiner 2004).

Morphological plasticity enables plants to maximize their fitness so that they are most suitable for present environmental conditions. This suggests that plasticity is useful when the environmental changes are moderate, and not so advantageous when the habitat is uniform or changing rapidly and in a large scale (Wijesinghe and Hutchings 1997). Plasticity is also more beneficial when environmental changes are predictable. Morphological changes are generally costly, so to avoid unnecessary waste of resources, plants must modify themselves faster than the environment changes (Levins 1968). Furthermore, plasticity is not beneficial when nutrients are scarce. Abundant nutrients supply plants with enough energy and materials to regenerate suitable organs and grow rapidly, otherwise plants can't express their capability of being plastic (Chapin 1980). Additional benefits of morphological plasticity arise when the plastic response can occur in later stages of growth and when the change is reversible (Alpert and Simms 2002).

The cost of plasticity begins with investments into the ability to perceive changing habitat conditions. For example, to assess changes in light climate, plants have to produce phytochromes – photoreceptors which can distinguish the ratio of incoming red and far-red radiation (Schmitt and Wulff 1993; Vandenbussche *et al.* 2005). As chloroplasts can absorb and utilize red, but not far-red radiation, vicinity of competitors may be perceivable for plants, through a lowered red:far-red radiation ratio in light reflected from neighbours, even before being shadowed (Aphalo *et al.* 1999). Decreased red:far-red ratio triggers changes in gene expression which, through hormones such as auxin, activate shade avoidance mechanisms – elongation of stems, positive phototropism (growth towards a light source) and hyponasty (upward bending of leaves) (Sandalio *et al.* 2016, Vandenbussche *et al.* 2005).

Plasticity can be realized through epigenetic mechanisms, especially what concerns DNA methylation. Epigenetically guided responses focus on hereditary phenotypic changes not mediated by variations in DNA chain. Instead, changes in DNA structure are present. For example, DNA methylation involves a methyl group that is added to DNA base cytosine or adenine (Dupont *et al.* 2009). DNA methylation affects the level of gene expression and therefore acts as a tool for phenotypic plasticity as it enables plants to adapt to environmental stress by designing the correct phenotype out of the genotype. As DNA methylation is hereditary, plants can

also prepare the next generation for current environmental conditions. At the same time, DNA methylation is easily reversible to allow the formation of the most suitable phenotype for the prevailing habitat status (Herrera and Bazaga 2013). It has been shown that heterophylly, “the concurrent variation in leaf form within a single plant” (Zotz *et al.* 2011), is epigenetically induced. Different leaf types on the same plant are produced by the same genotype, but in these contrasting leaf types, the level of DNA methylation differs. In *Ilex aquifolium*, prickly leaves have less methylated DNA than non-prickly leaves. The formation of prickly leaves is induced by herbivory, so it is safe to assume that epigenetics plays an important role in plant morphological plasticity (Herrera and Bazaga 2013).

Considering the cost of plasticity and the environmental requirements necessary for plasticity to be useful, it is obvious that plasticity is not the only strategy for obtaining maximum fitness. Hence, plants vary in their degree of plasticity. In a research by Lepik *et al.* (2005), they calculated shoot plasticity to light availability for 35 herbaceous species. For example, *Serratula tinctoria* and *Filipendula ulmaria* are practically non-plastic, whereas *Plantago lanceolata* and *Arrhenatherum elatius* are greatly plastic to light availability.

## 2. Plant morphological plasticity- effects on community level

Just as plastic morphological changes affect plant performance on individual level, plasticity poses an effect on the structure and diversity of plant communities (Lepik *et al.* 2005; Lepik *et al.* 2015; Ashton *et al.* 2010; Lipowsky *et al.* 2015; Burns and Strauss 2012; Nobel 1997; Schiffers *et al.* 2011; Grime and Hodgson 1987; Aerts *et al.* 1991; Bret-Harte *et al.* 2008; Molina-Montenegro *et al.* 2012). To further address the importance of morphological plasticity on species composition, recent studies frequently incorporate intraspecific trait variability in studying plant community dynamics (Violle *et al.* 2012; Bolnick *et al.* 2011; Kunstler *et al.* 2016; Abrams 1995; Lipowsky 2015). Plant morphological plasticity is undoubtedly an important source of intraspecific trait variability, therefore affecting community composition.

### 2.1. Competition

Plants, being sessile organisms, can-not actively select their habitat, they must make the most out of the current environment. For this reason, growing big and

doing it fast is generally the key to ecological success (Keddy *et al.* 2002). This leads to the prevalence of competition as one of the main interactions between plants (Keddy 1989). Competition can be defined as mutual negative effect between organisms which is caused by using the same limited resource (Tilman 1982). In plants, however, in addition to resources such as light and nutrients, competition for space is also substantial (Yodzis 1986). Two contrasting competition types, different in their function and location in space, can be distinguished. Above-ground competition, which is mainly competition for light, and below-ground competition, competition for nutrients and water (McPhee and Aarssen 2001). It is helpful to distinguish root and shoot competition to better understand the mechanisms of competition.

Goldberg (1990) suggested separating competitive effect and competitive response as two different strategies for increasing competitive ability. Competitive effect relies on increasing the impact on competitor plant mostly by increasing their biomass, both above-ground and below-ground, but also by expanding leaf width and leaf area (Keddy *et al.* 2002). Another method for enhancing competitive effect is by allelopathy. Allelochemicals are secondary metabolites which can have a negative impact on neighbouring organisms (Stamp 2003). For example, *Centaurea diffusa*, a successful invasive weed in North America, uses its secondary metabolite 8-hydroxyquinoline to chemically suppress local competing plant species. 8-hydroxyquinoline acts as a novel weapon in invaded communities, as North American species soil microbes may not have evolved natural resistance to the allelochemical. *C. diffusa*'s local communities in Eurasia are adapted to 8-hydroxyquinoline and therefore, *C. diffusa* is uncommon in its native range (Vivanco *et al.* 2004).

Competitive response reflects the ability of a species to resist suppression from its neighbours (Goldberg 1990). There are three main strategies to avoid or tolerate competition: escaping in time or space, foraging and persistence (Keddy *et al.* 1998). Plants escape from competition in time by shifting their phenology. For example, tallgrass prairie species have different flowering times so that competition for pollinators is decreased (Anderson and Schelfhout 1980). Escaping in space is possible by upward growth (Keddy *et al.* 1998), clonal dispersal or seed dispersal (Starfinger and Stöcklin 1996). Foraging response occurs by growing quickly



towards available resource patches, sequestering the resources, and continuing the rapid, controlled growth towards more available resources. Persistence response acts by surviving in unproductive habitats. Stress-tolerant plants have low relative growth rates and possess special adaptations for storing resources (Keddy *et al.* 1998).

Whether to rely on the effect or response depends on the properties of the limiting resource. Unevenly scattered soil nutrients can be harvested by growing long roots and exploiting the resource before competitors. This promotes the prevalence of competitive effect. Water, on the other hand, is spatially scattered more evenly than nutrients. Also, water availability generally can't be substantially increased by plants. Therefore, competitive response to tolerate water deficiency is preferred. Competition for light is successful when developing both competitive effect and response traits, as juvenile plants benefit from tolerating low light availability and adult plants benefit from outgrowing neighbouring plants, shading them instead (Craine and Dybzinski 2013).

To further understand competition and how it affects species composition, we must distinguish interspecific and intraspecific competition. The effect of competition on species coexistence is determined by the ratio of the strength of intraspecific to interspecific competition (Turcotte and Levine 2016). Generally, intraspecific competition is stronger than interspecific, as members of the same species have highly similar resource requirements and overlapping niches whereas different species have a smaller resource overlap, and thus niche overlap (Connell 1983). This brings us to the definition of ecological niche. According to Polechová and Storch (2008), "Ecological niche is a term for the position of a species within an ecosystem, describing both the range of conditions necessary for persistence of the species, and its ecological role in the ecosystem." As stated in Gause's competitive exclusion law, two species can coexist only when their niches do not completely overlap. If the ecological niches of the two species are extremely similar, sooner or later, one of the two species will go extinct (Gause 1934).

## 2.2. Species coexistence mechanisms

In the competitive world of plants, many coexistence mechanisms are responsible for maintaining local species richness. The latter function in two major ways, by stabilizing and equalizing. Stabilizing mechanisms are based on density dependant negative feedback. As the frequency of a species increases, the more it suppresses itself as intraspecific competition is usually stronger than interspecific competition. Equalizing mechanisms generally minimize average fitness differences between species (Chesson 2000). One possible equalizing mechanism is based on environmental heterogeneity. Each species exhibit the strongest competitive ability growing in an environment with a specific resource ratio. If the environment is heterogenous, multiple species can coexist (Tilman 1985). Another equalizing mechanism is stress. Species diversity relies on the amount of available resources and therefore productivity. If resources are scarce, only few species can survive. On the other end of the scale, abundant resources allow species to realize their competitive ability. Therefore, moderately stressful environment results in the highest species diversity (Al-Mufti *et al.* 1977). Herbivory and mowing act as another equalizing mechanism by equalizing competition for light. Herbivores and mowing repress potential dominants, at the same time promoting species with low competitive ability. Mowing with biomass removal also reduces the availability of nutrients such as nitrogen, which also promotes species coexistence (Kull and Zobel 1991; Maron and Jefferies 2001). Additional equalizing mechanism acts by parasitism or hemiparasitism. The presence of (hemi)parasites suppresses the growth of the host plant. For example, hemiparasitic herbaceous plant *Rhinanthus minor* gains some of its nutrients from the roots of neighbouring plants. Host selection is thought to be random and primarily a function of host root abundance and distribution within the soil profile. Therefore, dominant species are more affected by the hemiparasite and competition between plants is equalized (Westbury and Dunnett 2008).

The previously described equalizing coexistence mechanisms are based on a presumable stability of the environment. When we consider that the environment is dynamic, changing habitat conditions favour different species in distinct times and therefore, the coexistence of species becomes possible. Huston (1994) suggested the “dynamic equilibrium model”, which indicates that to achieve maximum species

diversity, the more productive the ecosystem, the stronger the frequency or intensity of the disturbance must be.

Certainly, competition is not the only type of relationship that plant species exhibit between one another. In highly stressful environments, a positive interaction, interspecific facilitation, plays an even greater role than competition (García-Cervigón *et al.* 2013). Facilitative interactions are encounters between organisms that benefit at least one of the participants and cause harm to neither one (Bruno *et al.* 2003). For example, in areas with periodic drought stress, increased aboveground biomass induced by higher plant diversity increases shade, which, consecutively, reduces surface drying and increases surface soil moisture, therefore improving surrounding microclimate (Wright *et al.* 2015). Another way interspecific facilitation operates is by increasing nutrient availability. Legumes, which can fix atmospheric nitrogen, can increase the local nitrogen pool, benefiting graminoids and herbs growing in vicinity of legumes (Spehn *et al.* 2002). As previously explained, this benefits species diversity only in areas with low local nitrogen pools, as moderately stressful environment results in the highest species diversity (Al-Mufti *et al.* 1977).

### **2.3. Plasticity may promote species coexistence**

Lepik *et al.* (2005) found a positive relationship between mean shoot plasticity of co-occurring species and ramet density. Since the number of species per unit area is a density dependant variable, species richness was also greater with increasing plasticity. They did not identify the mechanisms which lead to greater ramet density in highly plastic environments, but, in plots with higher mean shoot plasticity, canopy height variability was significantly lower. This refers to reduced competition for light by decreasing competition asymmetry, which comes from mutual adjustments in the number and shape of above-ground organs induced by reciprocal shading. Because plasticity enables plants to adapt with environmental fluctuations, in addition to decreased competition asymmetry, plasticity should increase ramet density by lowering neutral mortality. They also claim that the mechanism behind plasticity and community structure is very stable in time, because the regression between species diversity and species mean plasticity showed no change during the five-year study period. In another work by Lepik and Zobel (2015), they found that the average shoot plasticity of neighbouring plants had a small, but consistent positive effect on

species richness after accounting for the effect of ramet density. While most variation in small-scale diversity could be explained by local ramet density, they also found a significant density-independent effect of shoot plasticity on species richness. This gives the impulse to examine other ways besides high ramet density on how plasticity can promote species coexistence.

Another way for plasticity to promote species coexistence is by niche complementary. Niche complementarity predicts that species are more likely to coexist when they differ in their resource and space use (Chesson 2000). Ashton *et al.* (2010) showed that plants are plastic in their patterns of resource use. Plants were able to change their preferred form of nitrogen in response to competition. In the absence of competitors, all plants preferred nitrate to ammonium. When exposed to competition, plants with higher competitive ability switched to using the most abundant form of nitrogen – ammonia. This kind of resource partitioning can reduce competitive exclusion and even contribute to the perseverance of rarer and less plastic species. Lipowsky *et al.* (2015) showed that with increasing species richness, plants expressed specific plastic responses to possess unique functional trait combinations which are essential for niche complementary. With increasing species richness, forbs with different growth forms (reptant, rosulate, semirosulate) and developmental stages varied greatly in leaf traits such as leaf length, SLA (specific leaf area) or foliar stable carbon isotope ratios. Similar results were established by Burns and Strauss (2012), who demonstrated that plasticity results in trait divergence patterns in SLA and root:shoot ratio, which leads to niche partitioning, in turn possibly mediating species coexistence. Roscher *et al.* (2015) found that in legumes, with increasing plant diversity, niche separation increased in dimensions related to leaf size and morphology. The total extent of occupied niche space was also larger in mixtures when compared to monocultures. At the same time, niche separation decreased in dimensions related to height growth and space filling, minimizing average fitness differences. Thus, besides divergence of traits, convergence in traits related to plant growth can also promote species coexistence. Morphological plasticity can therefore act as an equalizing coexistence mechanism by balancing species fitness (see also Lepik *et al.* 2005). Furthermore, in distinct traits, both divergence and convergence can occur simultaneously, doubling the positive effect of morphological plasticity on species coexistence.

Examples of belowground niche separation and root territoriality are plentiful. Nobel (1997) studied three perennial desert codominants (*Encelia farinose*, *Pleuraphis rigida* and *Agave deserti*) with mean rooting depths of 9–10 cm for isolated plants. Compared with isolated plants, roots of adjacent interspecific plant pairs averaged 2-3 cm shallower for *Agave deserti* and 2-3 cm deeper for the other two species. This suggest partial separation of their root niches when plants are exposed to competition. Nobel also noted a temporal niche separation for water uptake. Another example of root territoriality demonstrated that study species *Bromus hordeaceus* responded plastically to intraspecific belowground competition by avoiding overlap of individuals' rhizospheres. Nutrient absorption was significantly lowered in proximity to other individuals and increased at the competitor-averted side (Schiffers *et al.* 2011).

In competitive environments, plasticity poses as a mechanism to enhance species competitive ability (Callaway *et al.* 2003). If greater competitive ability increases intraspecific competition more than interspecific competition, species coexistence is promoted. As previously mentioned, the effect of competition on species coexistence is determined by the ratio of the strength of intraspecific to interspecific competition (Turcotte and Levine 2016). Gersani *et al.* (2001) and Maina *et al.* (2002) showed that plasticity in root growth increases the strength of intraspecific competition. Plants overinvested in roots when exposed to conspecific neighbours. In theory, this could help to reduce competition between species.

#### **2.4. Plasticity may hinder species coexistence**

Simultaneously, there are theories and many examples of hindering effects of plasticity on plant species coexistence. Morphological plasticity, especially during the differentiation of leaves and roots, has the potential to increase the competitive ability of a plant (Grime and Hodgson 1987). Developmental plasticity of *Betula nana* allowed the species to become dominant when growing in fertilized soil. The number of branches and the rate of production of new meristems increased greatly, allowing extensive growth. This led to a development of a dense canopy, inflicting light limitation on the other co-dominant species (Bret-Harte *et al.* 2008). Aerts *et al.* (1991) found that plasticity enhances plant competitive ability in nutrient rich soil.

Plants high in morphological plasticity were able to increase their biomass at the expense of less plastic plants by spatially arranging leaf layers higher in the canopy and changing allocation patterns in favour of roots. Plasticity in resource use can also enhance competitive ability. For some plants, competition causes a change in the preferred form of nitrogen absorbed by roots, promoting their competitive ability by enhancing their total nitrogen uptake. At the same time, nitrogen uptake and thus growth of the less competitive and less plastic species could be inhibited (Ashton *et al.* 2010).

Additionally, plasticity can facilitate invasion success. Plasticity allows species to maintain efficient ecophysiological performance in changing environments. *Taraxacum officinale*, an invasive species in alpine regions, showed greater plasticity in many ecophysiological traits than the native species *Hypochaeris thrincioides*. For example, *T. officinale* showed greater foliar angle in high light intensity than *H. thrincioides*. As a result, *T. officinale* was able to perform better under harsh alpine climate conditions than native *H. thrincioides*. The invasive *T. Officinale* exerted strong competitive effects on *H. thrincioides*, depressing its biomass up to 59%. Greater plasticity may thus help explain the invasive success in changing and more stressful environments such as alpine regions (Molina-Montenegro *et al.* 2012).

### 3. Introduction to the experiment

Different studies held in the Laelatu wooded meadow in Estonia have shown that plant morphological plasticity to light availability promotes species diversity (Lepik *et al.* 2005; Lepik and Zobel 2015). To further explore the results, I decided to conduct an outdoor pot experiment with species from Laelatu wooded meadow, varying in their degree of plasticity. Each pot consisted of a four species community, different in their mean plasticity. To assess the effect of plasticity on species coexistence, amongst other measurements, I measured the evenness of abundance of the four species within each pot. Based on the previous results, I hypothesised that “Plasticity promotes species coexistence”.

## METHODS

In the autumn of 2017, I collected the seeds of 25 different species of forbs and graminoids growing in Laelatu wooded meadow located in West-Estonia. To cold stratify the seeds, I placed air dried seeds into a refrigerator for a few months. This simulates the natural temperature conditions that the seeds must encounter before germination can occur. At the beginning of spring I conducted a germination test to specify the exact species to use in my experiment. For the germination test I sowed 100 seeds from each species into sterilized sand. To increase the germination rate, I disinfected the seeds by soaking them in potassium permanganate solution for a minute. During the next consecutive weeks, I recorded how many of the sowed 100 seeds germinated. Considering the germination success and overall amount of seeds collected, I chose the following 18 herbaceous species for my experiment: *Filipendula ulmaria*, *Serratula tinctoria*, *Melica nutans*, *Molinia caerulea*, *Calamagrostis epigejos*, *Filipendula vulgaris*, *Prunella vulgaris*, *Sesleria caerulea*, *Briza media*, *Angelica sylvestris*, *Leontodon hispidus*, *Agrostis stolonifera*, *Festuca arundinacea*, *Achillea millefolium*, *Dactylis glomerata*, *Phleum pratense*, *Festuca rubra* and *Plantago media*. All those species have previously experimentally estimated value for shoot plasticity to light availability and plasticity indexes for specific traits (Lepik *et al.* 2005) (Additional materials, Table 1). In May 2018, I sowed disinfected seeds of the selected species into pots. Each pot contained three litres of 1:1 mixture of soil from Laelatu wooded meadow and sand. In each pot were four different plant species (Additional materials, Table 2). Considering the germination rate, I sowed so many seeds that ten individuals from each species would inhabit the pot. Therefore, in each pot, about 40 individual plants germinated. Before sowing the seeds, I distributed the pots into three categories according to the index of morphological plasticity: pots with high mean morphological plasticity; pots with low mean morphological plasticity; and mixed pots, where plants both high and low in morphological plasticity grew together. Each category contained 20 pots, so all in all the experiment held 60 pots. Within the category, all the species were selected randomly using R Studio (RStudio Team 2016).

In June and July, plants grew in a greenhouse in Järvelja. In the beginning of August, I placed the pots outside. Plants were watered as required, often three times

a day as the summer was extraordinarily hot. Throughout the summer, I removed the weeds and randomized the pots.

At the beginning of September, I started to measure different plant parameters. I evaluated the coverage of each species within a pot. I also evaluated moss coverage. The height of the tallest plant from each species was measured with a ruler. Then I cut the aboveground parts of the plants and placed up to ten ramets per species within a pot to individual minigrip bags for following measurements. To measure the leaf area, I scanned (Epson perfection V700 Photo) the biggest leaf of each collected ramet. To calculate the leaf area, I used a program WinRHIZO pro 2008 (Regent Instruments Canada Inc. 2008). After scanning the leaves, I dried plant aboveground biomass in a drying chamber for 48h in a 70°C heat. I weighed (Kern AEJ 200-4 CM) the biggest leaf, the petiole of the biggest leaf, and the rest of the plant from each species within a pot. If the species had grown more than ten ramets, I also weighed the remaining aboveground biomass. I counted the number of leaves from each ramet. If plants had any generative organs, I noted the number, length and weight of those. I found the specific leaf area (SLA,  $\text{cm}^2/\text{g}$ ) by dividing the area of the biggest leaf with its biomass.

To analyse the roots, I took four samples from each pot, using a soil drill 2,3 cm in diameter. After that, I washed the roots. Then I analysed the roots using WinRHIZO pro 2008. I found the specific root length ( $\text{cm}/\text{mg}$ ), root length (cm), root tissue density ( $\text{mg}/\text{cm}^3$ ), root area ( $\text{cm}^2$ ) and specific root area ( $\text{cm}^2/\text{g}$ ) for each pot. After that I dried the roots in a drying chamber for 48h in 70 °C and weighed the dry biomass of the roots.

Plasticity of different traits for all the species was previously calculated (Lepik, unpublished data) (Table 1). Plasticity of a plant morphological trait (T) in response to light availability (L; percent of full daylight) was defined as the absolute value of the slope of the reaction norm between T and L. The allometric effect of biomass was considered and removed and trait value was log-transformed (Lepik *et al.* 2005). Plasticity in traits explored in this experiment were plasticity in leaf number, leaf area, leaf length, SLA and root:shoot biomass ratio (Table 1).



Experimentally estimated shoot plasticity to light availability (P) was previously calculated (Lepik *et al.* 2005) as a combination of two different trait plasticities – leaf number and leaf area plasticity,

$$P = (P_{LA}^2 + P_{LN}^2)^{0,5},$$

where  $P_{LN}$  denotes plasticity of leaf number and  $P_{LA}$  plasticity of leaf area.

For each pot, I calculated the mean plasticity indexes and the variation coefficient of plasticity of the four species within a pot for all previously mentioned traits. I also calculated mean weighted plasticity for each pot as mean of each species plasticity multiplied with a species proportion of coverage or biomass from the whole pot's coverage or biomass. Weighted plasticity helps to understand the final plasticity within a pot at the end of the growing season.

I calculated delta plasticity, a difference between weighted plasticity and mean plasticity. The sign of delta plasticity indicates if the more plastic (+) or less plastic (-) species dominate the pot at the end of the growing season.

To describe species diversity, for each pot, I calculated the inverse value of the Simpson index  $N_2$  as

$$N_2 = 1 / \sum_{i=1}^N p_i^2$$

where N is the number of species in a pot and  $p_i$  the proportion of coverage or biomass of the i-th species.

Shannon index  $H'$  as

$$H' = - \sum_{i=1}^N p_i \ln p_i$$

where N is the number of species in a pot and  $p_i$  the proportion of coverage or biomass of the i-th species.

Hill's diversity index  $N_1$  as

$$N_1 = \exp^{H'}$$

And biomass-weighted evenness or coverage-weighted evenness of abundance  $E_{2,1}$  as

$$E_{2,1} = \frac{N_2}{N_1}$$

Evenness of abundance is a measure of the relative abundance of different species within a pot. The maximum value of evenness is 1. Evenness of abundance with a value of 1 implies that all species present within a pot have the same proportion of coverage or biomass, that the species community within a pot is equal. This indicates maximum diversity. The minimum value of evenness is 0.

For statistical analyses I used STATISTICA 7 (StatSoft Inc. 2007).

## RESULTS

In 58 pots out of 60, species richness remained constant throughout the experiment. In two pots, only three out of the four sowed species survived.

Highly plastic plants dominated three times more frequently than less plastic plants within a pot both in terms of biomass and coverage (Figure 1). In 78% of the pots (N=60), highly plastic plants dominated in biomass and in 69% of the pots in coverage. Less plastic plants dominate in 22% and 31% of pots accordingly. Results were tested with one-way chi-square analysis and proved significant (df=1;  $\chi^2=19,27$ ;  $p<0,0001$  for biomass and df=1;  $\chi^2=8,97$ ;  $p=0,0042$  for coverage).

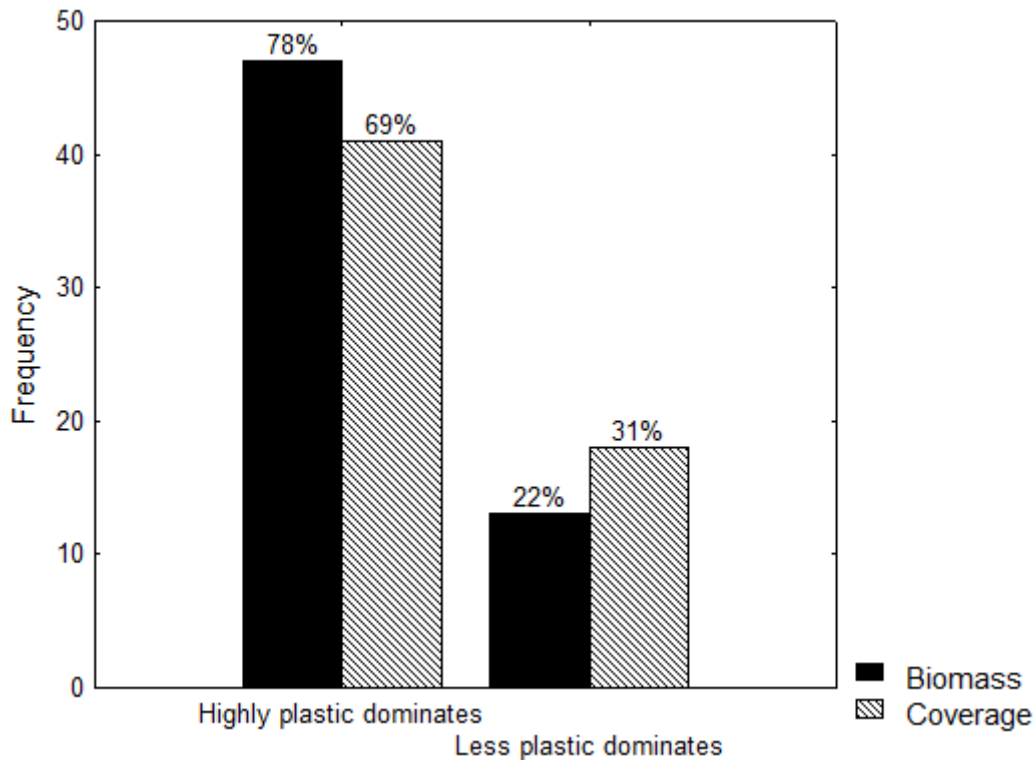


Figure 1. Histogram showing that species with high shoot plasticity to light availability from each pot (N=60) dominate three times more frequently over less plastic plants both in biomass and coverage.  $\chi^2$  test proved that the results are significant (df=1;  $\chi^2=19,27$ ;  $p<0,0001$  for biomass and df=1;  $\chi^2=8,97$ ;  $p=0,0042$  for coverage).

I did not find a significant correlation between biomass-based evenness of abundance and any of the plasticity indexes, but I did find many significant correlations between coverage-based evenness of abundance and many plasticity indexes such as plasticity in specific leaf area, mean leaf number plasticity and mean leaf length plasticity. There was a negative correlation ( $r^2=0,2244$ ;  $p=0,0001$ ) between plasticity in specific leaf area and coverage-based evenness of abundance (Figure 2). When plasticity in specific leaf area was weighted with coverage, the correlation became even stronger ( $r^2=0,5947$ ;  $p<0,0001$ ) (Figure 3). The greater the mean community plasticity in specific leaf area, the less even the community was.

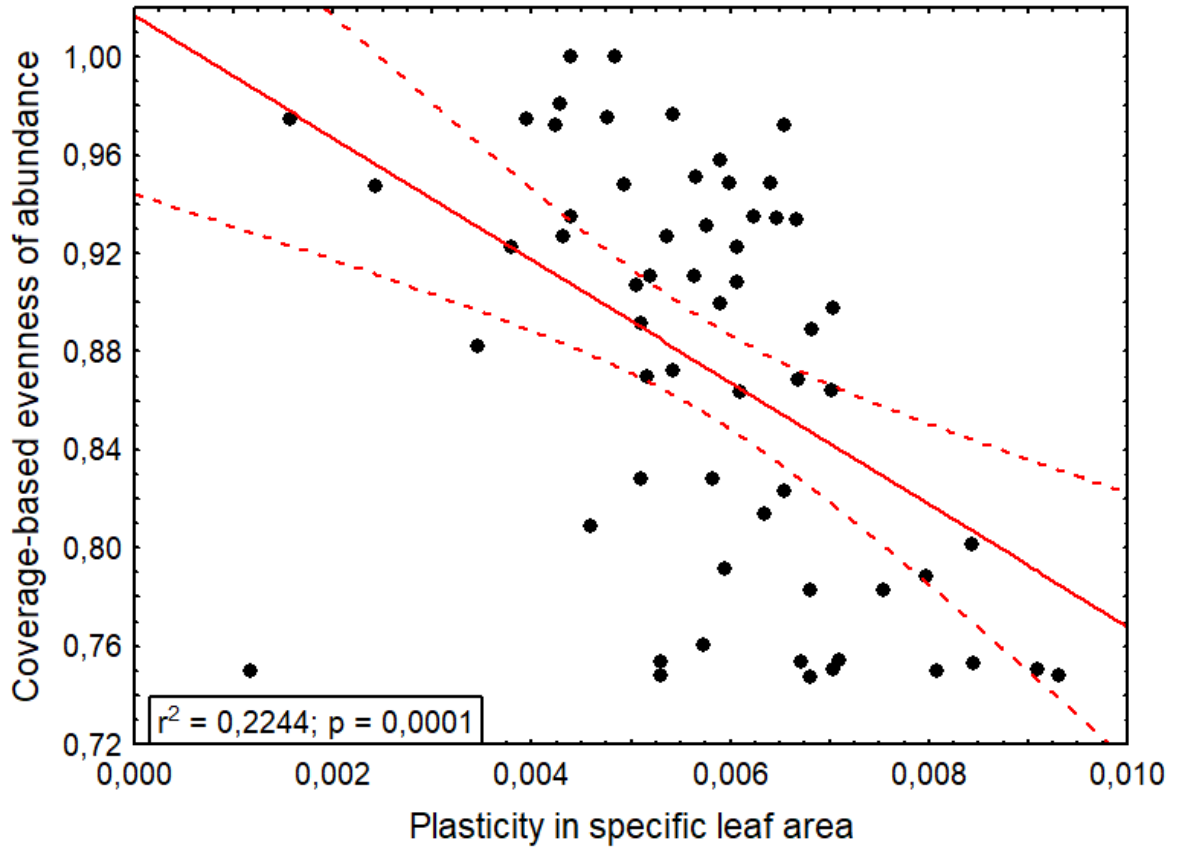


Figure 2. Negative correlation between pot mean specific leaf area plasticity and coverage-based abundance evenness ( $r^2=0,2244$ ;  $p=0,0001$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

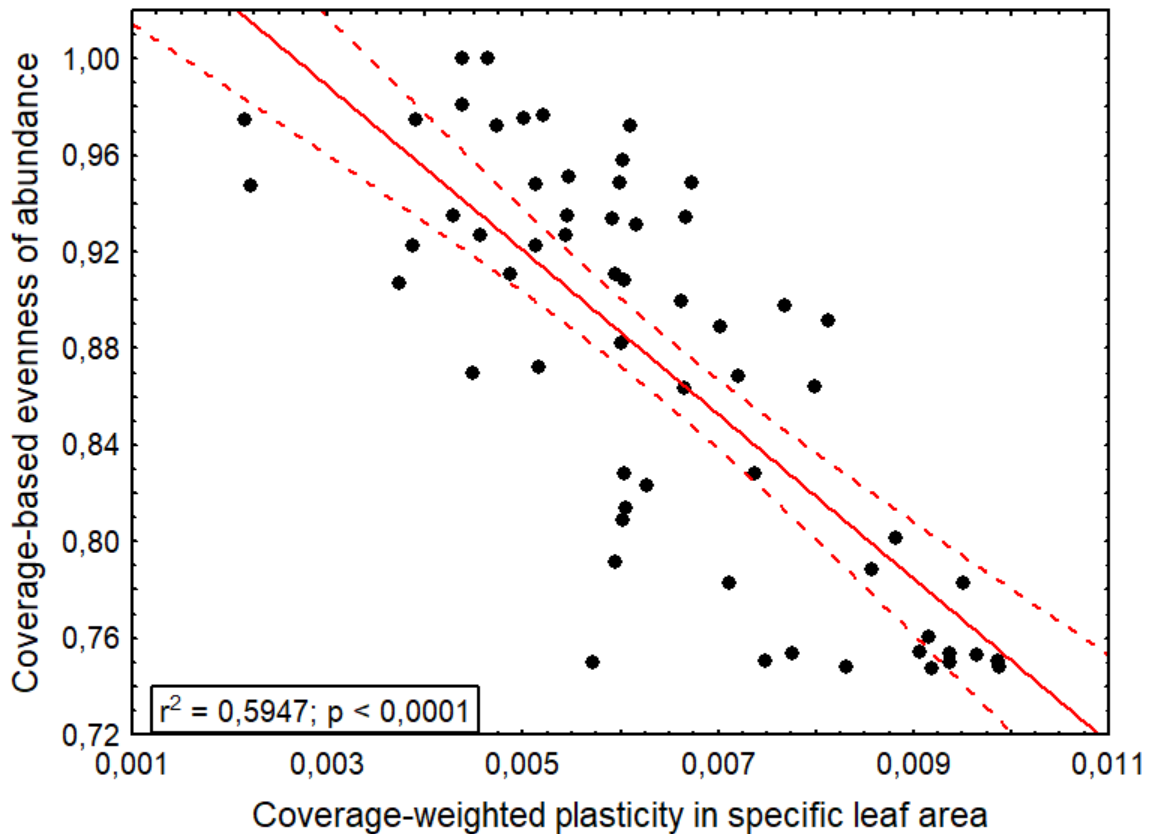


Figure 3. Negative correlation between coverage-weighted specific leaf area plasticity and coverage-based evenness ( $r^2=0,5947$ ;  $p<0,0001$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

There was a significant positive correlation ( $r^2=0,2155$ ;  $p=0,0002$ ) between pot mean plasticity in leaf number and coverage-based evenness (Figure 4). As before, the correlation between plasticity in leaf number and coverage evenness was stronger ( $r^2=0,2842$ ;  $p<0,0001$ ) when plasticity in leaf number was weighted with coverage (Figure 5). This means that the greater the mean community plasticity in leaf number, the more even the community is. The smaller the mean community plasticity in leaf number, the more unproportional the species diversity within a pot.

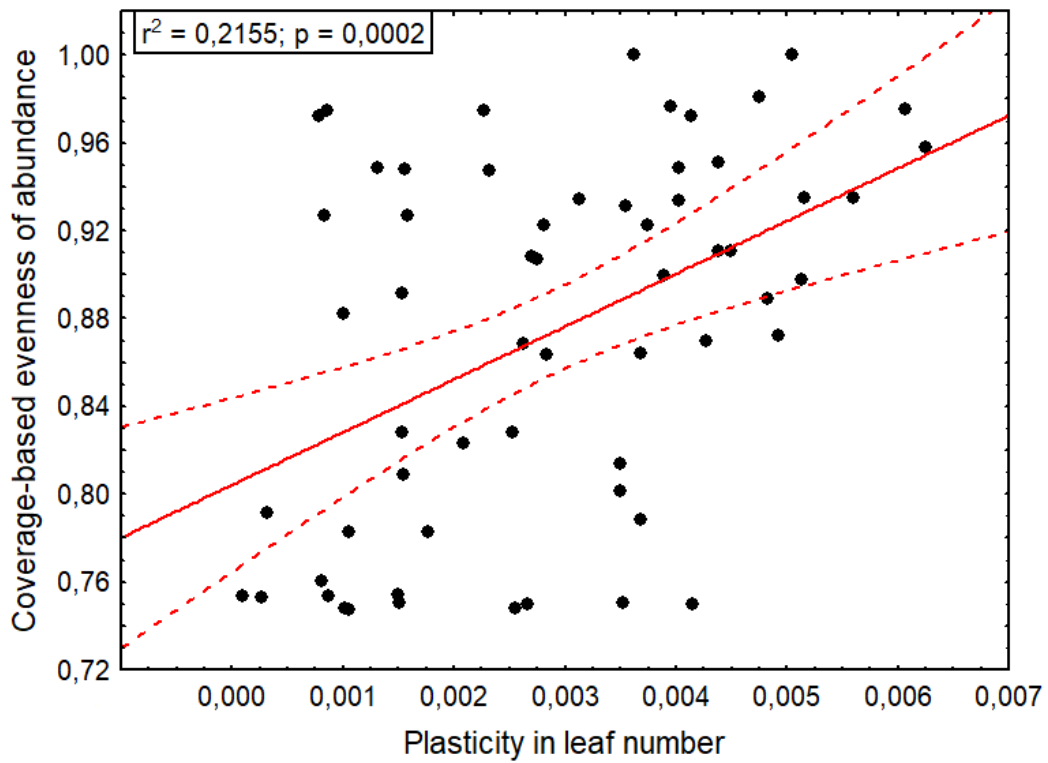


Figure 4. Positive correlation between pot mean plasticity in leaf number and coverage-based evenness ( $r^2=0,2155$ ;  $p=0,0002$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

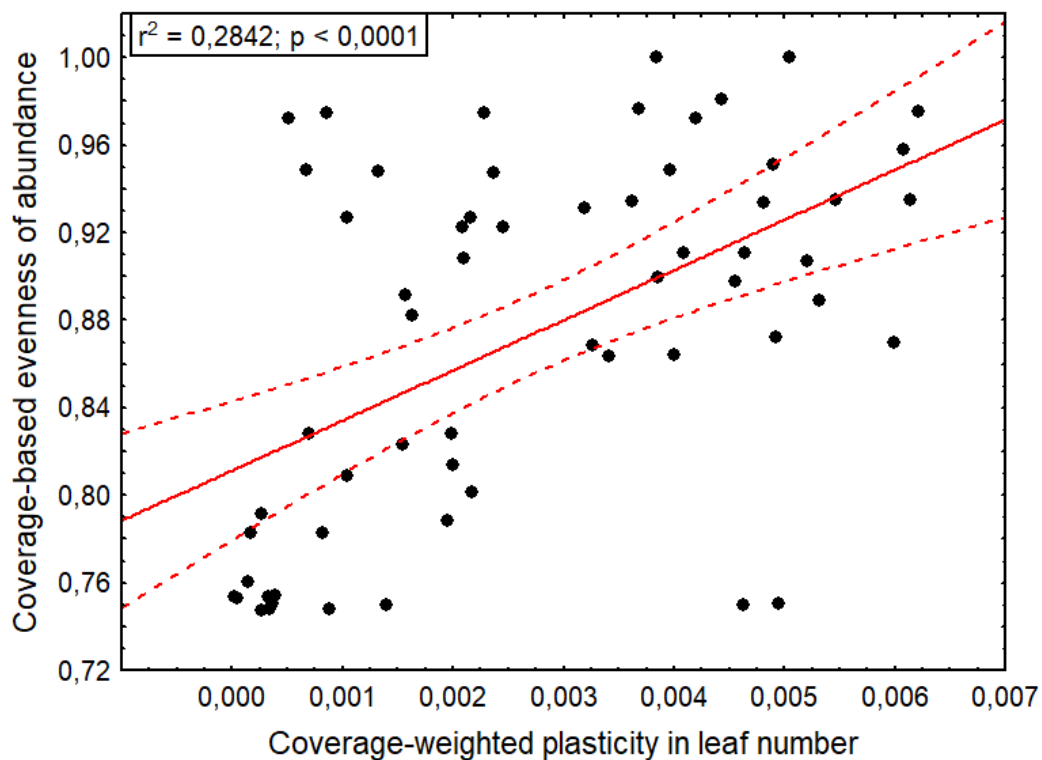


Figure 5. Positive correlation between pot mean coverage-weighted plasticity in leaf number and coverage-based evenness ( $r^2=0,2842$ ;  $p<0,0001$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

There was a significant positive correlation ( $r^2=0,1238$ ;  $p=0,0058$ ) between pot mean plasticity in leaf length and coverage-based evenness (Figure 6). There was an even stronger positive correlation ( $r^2=0,2532$ ;  $p<0,0001$ ) between pot mean coverage-weighted plasticity in leaf length and coverage-based evenness (Figure 7). The greater the pot mean plasticity in leaf number, the more proportional the coverage of each of the species within a pot was. Additionally, as all correlations beforehand signify, it is important to weigh the plasticity indexes to get the most accurate results.

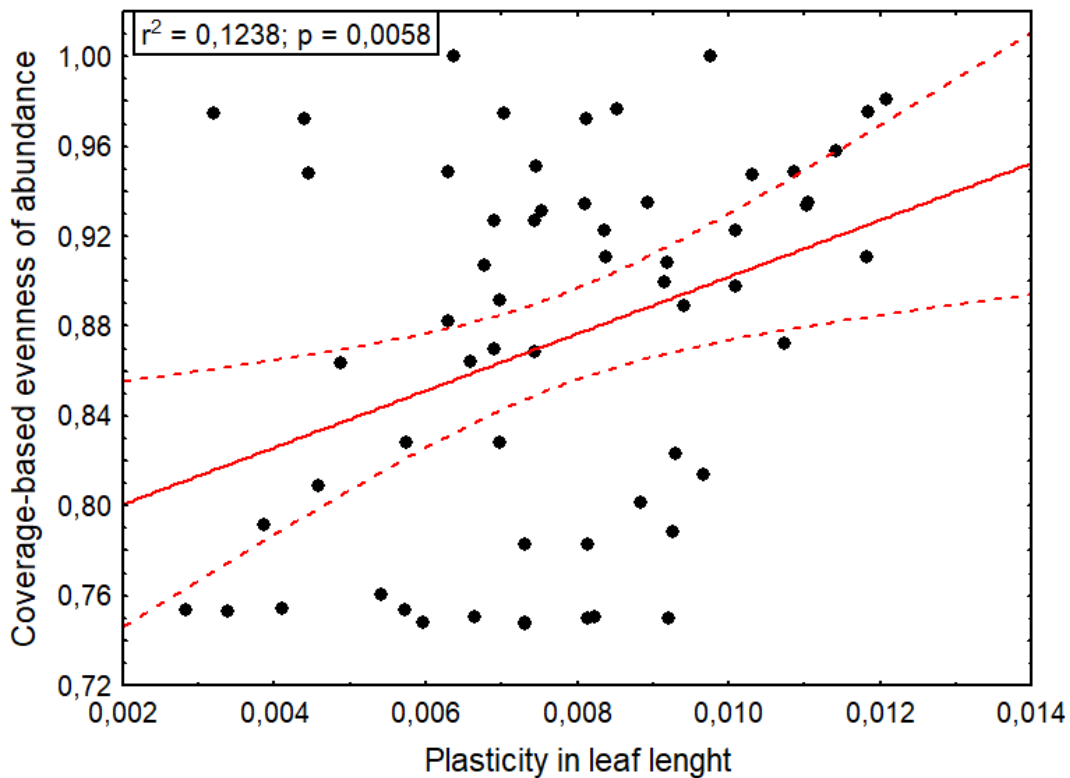


Figure 6. Positive correlation between pot mean plasticity in leaf length and coverage-based evenness ( $r^2=0,1238$ ;  $p=0,0058$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

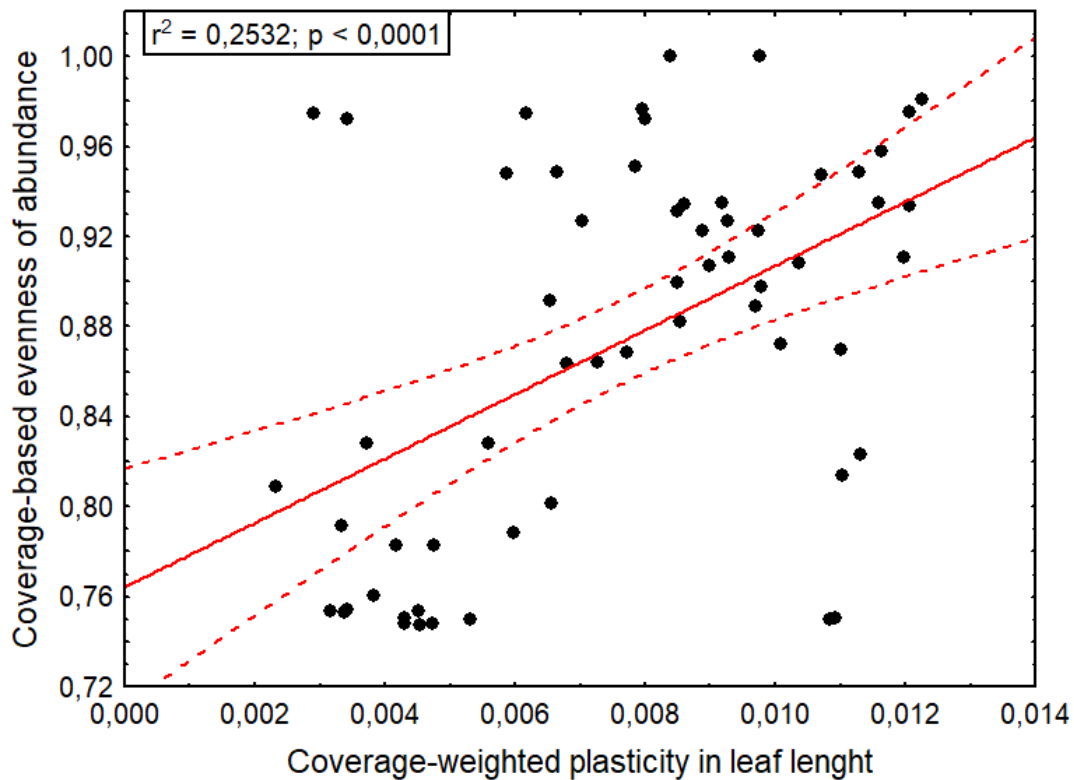


Figure 7. Positive correlation between pot mean coverage-weighted plasticity in leaf length and coverage-based evenness ( $r^2=0,2532$ ;  $p<0,0001$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

Pot mean shoot plasticity to light availability was positively correlated ( $r^2=0,1762$ ;  $p<0,0008$ ;  $N=60$ ) with coverage-based evenness (Figure 8). Mean shoot plasticity to light availability is a combined index of plasticity from plasticity in leaf number and plasticity in leaf area (more detailed description available in METHODS section). The greater the pot mean shoot plasticity to light availability, the greater the coverage evenness within a pot.



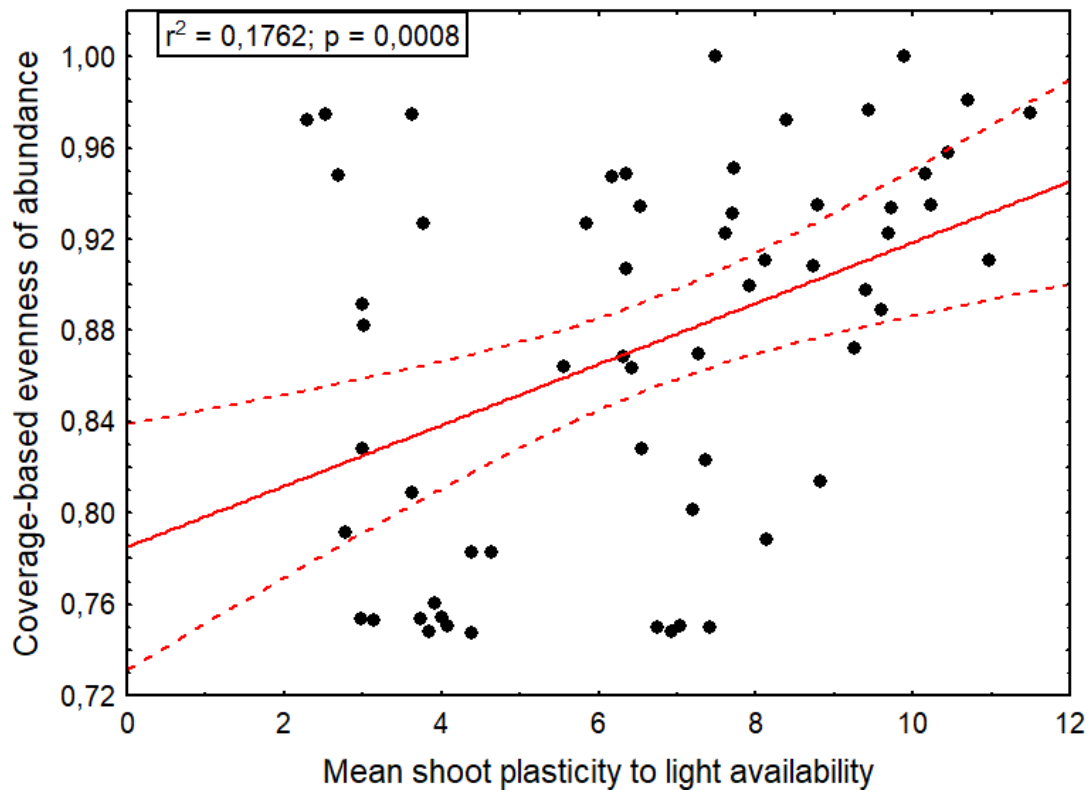


Figure 8. Positive correlation between pot mean shoot plasticity to light availability ( $P \cdot 10^{-4}$ ) and coverage-based evenness ( $r^2=0,1762$ ;  $p=0,0008$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

Another interesting result incorporates the coefficient of variation of different trait plasticity indexes. For example, there was a negative correlation ( $r^2=0,2351$ ;  $p<0,0001$ ) between the coefficient of variation of plasticity in root:shoot biomass ratio and coverage-based evenness (Figure 9). I found similar, but slightly less descriptive results with other plasticity indexes such as plasticity in leaf number ( $r^2=0,1543$ ;  $p=0,002$ ) and plasticity in leaf length ( $r^2=0,0725$ ;  $p=0,038$ ). This means that the more the plasticity index varies within a pot, the less proportional the coverage of each species is. If species within a pot have a more similar index of plasticity, the community coverage is more even.

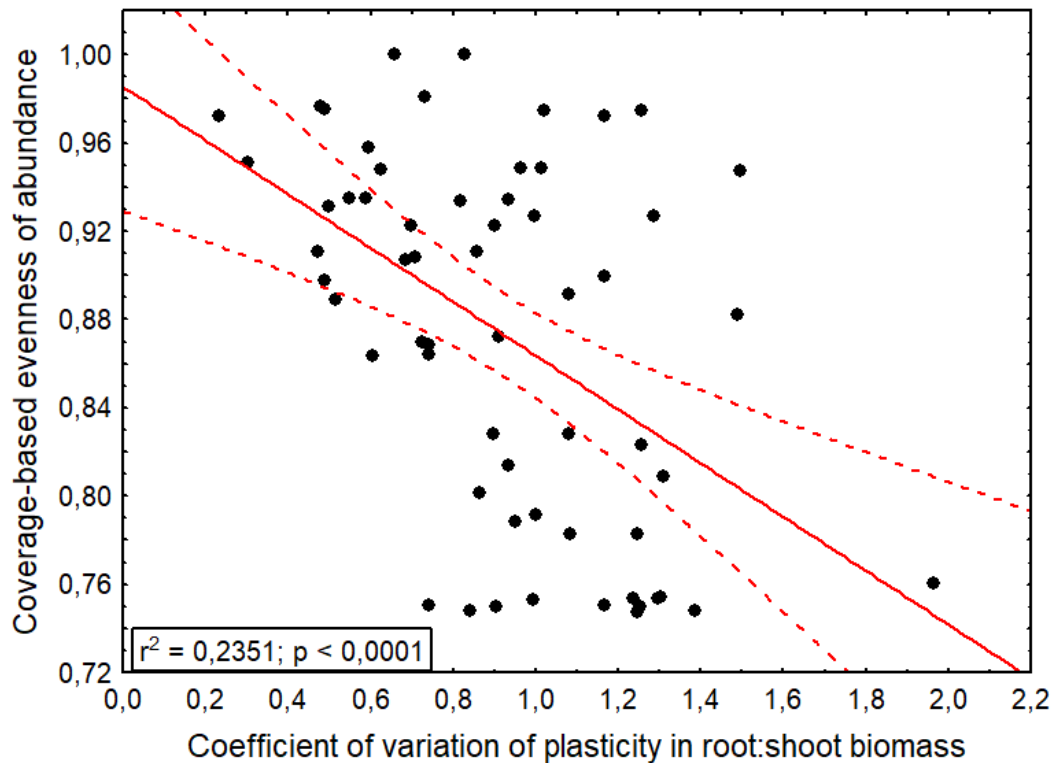


Figure 9. Negative correlation between coefficient of variation of plasticity in root:shoot biomass within a pot and coverage-based evenness ( $r^2=0,2351$ ;  $p<0,0001$ ;  $N=60$ ). Dotted confidence bands confine the area that has a 95% chance of containing the true regression line.

## DISCUSSION

As demonstrated in Figure 1, plants with high shoot plasticity to light availability dominated over less plastic plants within a pot in 69% of the pots in terms of coverage and in 78% of the pots regarding biomass. Those results imply that plasticity can enhance species competitive ability, therefore hindering species coexistence. Figure 2 and 3 imply the same, showing the surprising results that the greater the pot mean plasticity in specific leaf area, the less even the community coverage. When species with high plasticity in specific leaf area happened to grow beside one another, definite dominant or dominants stood out and community diversity was low. Interestingly, in works by Lepik and Zobel (Lepik *et al.* 2005; Lepik and Zobel 2015), plasticity in specific leaf area is ignored in describing the relationship between community composition and morphological plasticity.

On the other hand, in concordance with the hypothesis “plasticity promotes species coexistence”, plasticity in leaf number, plasticity in leaf length and shoot plasticity to

light availability seem to promote species coexistence, as greater pot mean plasticity in those indexes resulted in more even community coverage (Figure 4 to 8). It can only be hypothesized through what mechanisms does plasticity in those traits promote coexistence in this experiment.

The beneficial effects of plasticity on community may arise through the plastic plants' ability to avoid competition. As plants can sense decreasing light conditions induced by neighbouring plants, especially decreased red:far-red radiation ratio, plastic plants are known to reduce branching and keep away from neighbours. In dense stands, instead of confrontation, plants choose to avoid competition (Herben and Novoplansky 2010). This lessens the overall competitive effect on the community, promoting species evenness.

Plasticity could help to decrease competition asymmetry by equalizing fitness mechanisms. Equalizing mechanisms minimize average fitness differences between species (Chesson 2000). It has been shown that convergence in traits related to plant growth promote species coexistence (Roscher *et al.* 2015). In this experiment, the coefficient of variation of the height of the highest specimen from each of the four species within a pot did not correlate with biomass-based nor coverage-based evenness of abundance. Therefore, in this case, this theory is probably not applicable. Unfortunately, I measured only the very highest plant from each species. Results could have been different when a bigger sample of plants from each species within a pot had been assessed.

Another way for plasticity to impact taxonomic diversity is by niche complementarity. Morphological plasticity can promote species coexistence by separating species niches. As many studies have found (Jucker *et al.* 2015; Lipowsky *et al.* 2015; Nobel 1997; Roscher *et al.* 2015; Schiffers *et al.* 2011), in a species rich community, plants express specific plastic responses to possess unique functional trait combinations by varying branching patterns and rooting depth, also varying in traits such as leaf length and specific leaf area, all to promote niche complementarity. This way, plants can maximise local resource acquisition and the community is able to sustain more species.

Plasticity may assist plants, and therefore the whole plant community with one of the competitive response strategies – persistence. Competitive response reflects

the ability of a species to resist suppression from its neighbours and persistence encourages surviving in unproductive habitats. Plasticity may allow plants to handle the stress of growing in dense, species rich communities where space, light, water and nutrients are scarce because competitive stress from neighbouring plants is high. Additionally, highly plastic plants have a reduced overall mortality as they are more adapted to changing environmental conditions. In this experiment, in 58 pots out of 60, species richness remained constant throughout the experiment. In two pots, only three out of the four sowed species survived. The two species that disappeared are *Calamagrostis epigejos* and *Molinia caerulea*, both with relatively low plasticity indexes. Given the sample size of the evidence, the conclusions based on this evidence may be coincidental.

Another possible strategy comes to mind when regarding the beneficial effects of plasticity on a community. The previously conducted experiments exhibiting positive relationship between community plasticity and species richness were conducted in the Laelatu wooded meadow (Lepik *et al.* 2005; Lepik and Zobel 2015), one that is mowed once a year (every summer in July). As previously mentioned, mowing acts as an equalizing coexistence mechanism, which represses potential dominants, at the same time promoting species with low competitive ability (Kull and Zobel 1991; Maron and Jefferies 2001). It is possible that plasticity helps to overcome and adapt to the stress of annual mowing, therefore promoting local species diversity. As the results from this experiment were based on one growing season, this theory is not applicable in this instance.

Another interesting find is the negative correlation between variation of coefficient of different plasticity indexes within a pot and pot coverage-based evenness (Figure 9). The more similar the species within a community are in their plasticity, the greater the coverage-based evenness of the pot. It seems like plants can possess one of the two strategies – being plastic or non-plastic, whereas the community thrives when plants can “agree” on a specific strategy. Interestingly, for taxonomic diversity, it is not important whether the pot mean plasticity is high or low. The same results concerning coefficient of variation and biomass-based evenness were found previously in my bachelors’ thesis.

The posed hypothesis “Plasticity promotes species coexistence” proved inconclusive. The hypothesis is true for leaf length and leaf number plasticity, as in shoot plasticity to light availability, as pots containing a community with higher mean plasticity had higher coverage-based evenness. The hypotheses proved false with specific leaf area plasticity, as pots with higher mean plasticity had lower coverage-based evenness.

## CONCLUSIONS

Morphological plasticity is the ability of a given genotype to produce diverse morphological phenotypes in response to varying environmental conditions (Callaway *et al.* 2003). Plasticity’s sole reason is to maximise the fitness of a plant, but it also poses an effect on plant community level. Morphological plasticity can promote species coexistence by increasing ramet density by means of shade-avoidance syndrome and decreasing competition asymmetry or by decreasing natural mortality. Morphological plasticity can also facilitate species coexistence by niche complementary and increasing the strength of intraspecific competition over interspecific competition by enhancing competitive ability. Morphological plasticity can also hinder species coexistence by increasing species competitive ability when it results in increased competition asymmetry. Plasticity can even facilitate invasion success, as plasticity allows plants to adapt to various climatic conditions prevalent outside their native range.

In this thesis, I posed an hypothesis “Plasticity promotes species coexistence”, which proved inconclusive. Plasticity in traits such as leaf length and leaf number, as well as shoot plasticity to light availability, which is a combined plasticity index of leaf area and leaf number, promoted species coexistence by increasing coverage-based evenness, but, surprisingly, plasticity in specific leaf area hindered coverage-based evenness and therefore, species coexistence. I also found reoccurring results concerning the coefficient of variation of different plasticity indexes within a community on coverage evenness. Plant morphological plasticity proved again to be a complex phenomenon, but it clearly poses an effect on community composition.

## ACKNOWLEDGEMENTS

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## ADDITIONAL MATHERIALS

**Table 1.** Species plasticity indexes of different traits. Shoot plasticity to light availability is calculated as  $P = (P_{LA}^2 + P_{LN}^2)^{0.5}$ , where  $P_{LA}$  is plasticity in leaf area and  $P_{LN}$  is plasticity in leaf number. Plasticity of plant morphological trait (T) in response to light availability (L; percent of full daylight) was defined as the absolute value of the slope of the reaction norm between T and L. The allometric effect of biomass was considered and removed and trait value was log-transformed. The elaboration of species abbreviations are *Fil ulm* (*Filipendula ulmaria*), *Ser tin* (*Serratula tinctoria*), *Mel nut* (*Melica nutans*), *Mol cae* (*Molinia caerulea*), *Cal epi* (*Calamagrostis epigejos*), *Fil vul* (*Filipendula vulgaris*), *Pru vul* (*Prunella vulgaris*), *Ses cae* (*Sesleria caerulea*), *Bri med* (*Briza media*), *Ang syl* (*Angelica sylvestris*), *Leo his* (*Leontodon hispidus*), *Agr sto* (*Agrostis stolonifera*), *Fes aru* (*Festuca arundinacea*), *Ach mil* (*Achillea millefolium*), *Dac glo* (*Dactylis glomerate*), *Phl pra* (*Phleum pratense*), *Fes rub* (*Festuca rubra*) and *Pla med* (*Plantago media*).

	Shoot plasticity to light availability	Plasticity in leaf number	Plasticity in leaf area	Plasticity in leaf lenght	Plasticity in SLA	Plasticity in root:shoot biomass
<i>Fil ulm</i>	0,00001	0,00011	0	0,00495	0,006	0,00023
<i>Ser tin</i>	0,000076	0	0,00076	0,00014	0,01	0,003
<i>Mel nut</i>	0,000291	0,00019	0,00291	0,00555	0	0
<i>Mol cae</i>	0,000327	0,00295	0,0014	0,00032	0,00542	0,0023
<i>Cal epi</i>	0,00036	0,00087	0,00445	0,00775	0,006895	0,0010545
<i>Fil vul</i>	0,000382	0,000175	0,002835	0,002	0,00687	0,0053135
<i>Pru vul</i>	0,00044	0	0,0044	0,0036	0,01	0,00002
<i>Ses cae</i>	0,000451	0,00285	0,001825	0,01047	0,006072	0,0000505
<i>Bri med</i>	0,000663	0,00317	0,00582	0,01236	0,01031	0,002
<i>Ang syl</i>	0,000679	0,00318	0,006	0,00703	0,009	0,004093
<i>Leo his</i>	0,0007	0,0023	0,0049	0,005	0,002	0,0030345
<i>Agr sto</i>	0,000768	0,00577	0,00507	0,00855	0,0076	0,004462
<i>Fes aru</i>	0,0009	0	0,00901	0,01287	0,00566	0
<i>Ach mil</i>	0,00094	0,00628	0,007	0,00921	0,004	0,0063
<i>Dac glo</i>	0,001096	0,007648	0,009226	0,01234	0,004422	0,0016384
<i>Phl pra</i>	0,001104	0,00629	0,00788	0,01294	0,00395	0,001124
<i>Fes rub</i>	0,001183	0,005046	0,00325	0,01019	0,0031	0,0009776
<i>Pla med</i>	0,001213	0,0053	0,01091	0,01187	0,0076	0,002717

**Table 2.** Species combination in each pot. The elaboration of species abbreviations are *Fil ulm* (*Filipendula ulmaria*), *Ser tin* (*Serratula tinctoria*), *Mel nut* (*Melica nutans*), *Mol cae* (*Molinia caerulea*), *Cal epi* (*Calamagrostis epigejos*), *Fil vul* (*Filipendula vulgaris*), *Pru vul* (*Prunella vulgaris*), *Ses cae* (*Sesleria caerulea*), *Bri med* (*Briza media*), *Ang syl* (*Angelica sylvestris*), *Leo his* (*Leontodon hispidus*), *Agr sto* (*Agrostis stolonifera*), *Fes aru* (*Festuca arundinacea*), *Ach mil* (*Achillea millefolium*), *Dac glo* (*Dactylis glomerate*), *Phl pra* (*Phleum pratense*), *Fes rub* (*Festuca rubra*) and *Pla med* (*Plantago media*).

Pot number	Species 1	Species 2	Species 3	Species 4	Pot number	Species 1	Species 2	Species 3	Species 4
1	pru vul	bri med	cal epi	ser tin	31	ses cae	fil ulm	phl pra	fes aru
2	ser tin	bri med	fil ulm	mol cae	32	fil ulm	mel nut	pla med	fes rub
3	fil ulm	bri med	ser tin	ses cae	33	bri med	pru vul	dac glo	ang syl
4	ses cae	mel nut	mol cae	fil vul	34	cal epi	fil vul	dac glo	leo his
5	pru vul	ses cae	bri med	ser tin	35	pru vul	fil vul	dac glo	leo his
6	mel nut	cal epi	bri med	pru vul	36	mol cae	fil vul	phl pra	fes rub
7	ses cae	fil vul	mel nut	pru vul	37	fil vul	ses cae	pla med	agr sto
8	pru vul	mel nut	fil vul	ser tin	38	fil vul	cal epi	phl pra	ang syl
9	cal epi	mel nut	ser tin	fil vul	39	ses cae	mol cae	agr sto	ang syl
10	pru vul	bri med	cal epi	mel nut	40	ser tin	fil vul	fes rub	fes aru
11	fil vul	fil ulm	mel nut	mol cae	41	ses cae	fil vul	ang syl	phl pra
12	fil ulm	bri med	ses cae	fil vul	42	cal epi	mol cae	pla med	fes rub
13	ses cae	fil vul	cal epi	bri med	43	pru vul	bri med	ach mil	pla med
14	mol cae	fil ulm	ses cae	bri med	44	pru vul	ses cae	leo his	fes rub
15	mol cae	ses cae	pru vul	fil vul	45	fil vul	mol cae	phl pra	dac glo
16	pla med	fes rub	ang syl	agr sto	46	fil vul	ses cae	ser tin	fil ulm
17	dac glo	fes aru	fes rub	pla med	47	fil vul	cal epi	pru vul	ser tin
18	agr sto	ang syl	leo his	pla med	48	ser tin	fil ulm	ses cae	bri med
19	fes aru	dac glo	pla med	ang syl	49	bri med	pru vul	fil vul	fil ulm
20	agr sto	fes rub	ang syl	fes aru	50	fil vul	fil ulm	cal epi	ses cae
21	fes rub	dac glo	phl pra	pla med	51	phl pra	pla med	ach mil	leo his
22	fes aru	agr sto	pla med	fes rub	52	leo his	pla med	ang syl	fes aru
23	ang syl	leo his	agr sto	ach mil	53	ang syl	pla med	leo his	fes rub
24	fes rub	dac glo	phl pra	fes aru	54	agr sto	phl pra	leo his	ang syl
25	fes aru	ang syl	leo his	agr sto	55	ach mil	dac glo	fes aru	agr sto
26	dac glo	leo his	fes rub	fes aru	56	cal epi	fil vul	fes aru	leo his
27	pla med	agr sto	dac glo	phl pra	57	pru vul	ses cae	fes rub	dac glo
28	dac glo	phl pra	ang syl	pla med	58	ses cae	fil vul	fes aru	pla med
29	ach mil	leo his	agr sto	phl pra	59	fil vul	mol cae	ang syl	fes rub
30	pla med	agr sto	phl pra	ang syl	60	pru vul	bri med	dac glo	agr sto

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