University of South Bohemia in České Budějovice
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Changes in plant composition and diversity depending on previous and current management types in riparian forests at the confluence of rivers Morava and Dyje: phytocenological analysis at the gradients of light and moisture conditions.

Bachelor thesis

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Annotation:

Effects of various past and present management types on plant composition and diversity were examined in the species rich area at the confluence of rivers Morava and Dyje. A phytocenological analysis was supplemented with information about water and light conditions. Plant composition regarding residence time and invasive statuses was also examined for each management type.

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Table of Contents

1. Introduction

1.1 What is a riparian forest?

Riparian or floodplain forests are forests at alluvial areas. They function as ecotones between aquatic and terrestrial ecosystems. Natural riparian forests are among the most diverse and dynamic terrestrial ecosystems and also belong to one of the most productive (Cartisano et al. 2013). They are a mosaic of landforms and communities encompassing sharp ecological gradients. Therein lays the source of the ecological complexity (Naiman et al. 1993; Maděra et al. 2011).

The word „riparian“ derives from the Latin term „*riparious*“ meaning „bank“. This would suggest that riparian forests are simply forests on land adjacent to a river. However the definition nowadays is stretched further. In simple terms when defining the area of the riparian forest we need to take into consideration areas up slope that are influenced by the river phenomenon as well as the aquatic ecosystem. While in theory simple, one encounters problems when attempting to accurately outline (for example on a map) the riparian area (Ilhadrt et al. 2000; Verry et al. 2004). Verry et al. (2004) defines this area of interest as the floodprone width of the valley plus 30 meters on each side and 15 meters around obvious landslides.

1.2 Types of riparian forest in Central Europe

Various types of floodplain forests occur in the alluvium of wide lowland rivers based on changing site conditions (Maděra et al. 2011). While there are many classifications available for riparian forests of Central Europe, that are applicable for the Czech Republic, it seems practical to stick to one of them. The main ecological factors determining species composition in riparian forests are the height of groundwater table, the presence and duration of floods (Gonzáles et al. 2010) and the type of soil. Each community type has its umbrella species, species key to understanding and properly designing management approaches for the community (Roberge et Angelstam 2004). Classification system based on Maděra (2011) is presented here, for which the most useful umbrella species seem to be woody vascular plant species.

A young development stage of riparian forests is called *Saliceta albae*. It grows on fresh riparian sediments in the convex bank parts of meanders. Its umbrella species is White

Willow (*Salix alba*). As an r-strategic plant it can spread quickly and is able to survive flooded for many months.

Another community type exists in close proximity to the river called *Ulmi-fraxineta populi*. Located on sandy sediments we can observe the communities on banks around the stream. Its umbrella species is Black Poplar (*Populus nigra*). Other poplar species are also present such as the White Poplar (*P. alba)* and its hybrid species Grey Poplar (*P. x canescens*). Similarly to the previous community type, it suffers from river regulations as its existence is dependent on regular sandy sedimentations. Both poplars and willows are pioneer species, establishing first on newly created land as mentioned in the two community types above (Gonzáles et al. 2010). Foundation species are crucial in creating locally stable environment and thus mediating important ecosystem services making possible further development towards later succession community types (Stella et al. 2011).

A community type specific to banks of grounded riverine lakes is called *Alni glutinosae-saliceta*. With river regulations the meandering process along with the creation of riverine lakes is eliminated. However similar lakes can be dug up to supplement the meandering process and help these communities. The umbrella species here is Common Alder (*Alnus glutinosa*).

A hardwood community dependent on high levels of underground water is called *Querci roboris-fraxineta*. It is the most typical hardwood riparian community with Pedunculate Oak (*Quercus robur*) as its dominant species.

The driest of the hardwood communities is called *Ulmi-fraxineta carpini*. It is generally not flooded and the underground water levels are below 150 cm. The umbrella species of this community is the European White Elm (*Ulmus laevis*). Another species of this genus, The Field Elm (*U. minor*) is also present. Both of these elms are suffering from Dutch Elm disease (Ďurkovič et al. 2013) that damages the trees and they are only able to survive by creating root stools. Dutch Elm disease must be acknowledged when planning management for this type of riparian forest. Elms also naturally have a solitary distribution rarely forming pure stands (Stoyanov 2004). This type of forest is covering more and more land due to river regulations as the alluvial areas get drier (Gonzáles et al. 2010, Stella et al. 2012).

1.3 Why are riparian forests worth protecting?

Riparian forests can provide many ecosystem services to their surroundings. They can serve as a nutrient sink, an area where import of nutrients is lower than export. Various soil organisms and plants in the riparian forests take up the nutrients and these are also deposited in the soil (Forshay et Stanley 2005, Hood et Naiman 2000). As nutrients such as nitrogen or phosphorus flow from the upland forests, riparian areas serve as a buffer zone that helps mediate the transfer of nutrients to the river and thus reduce the effects of eutrophication (Cirmo et al. 1997). Denitrification, a process of transforming nitrogen into a less available form, is three times faster in riparian forests compared to an upland forest which is probably caused by higher moisture and therefore lower oxygen availability as well as by lower temperature thanks to the shadow (Schipper et al. 1993). Furthermore, after clear felling of forests we can observe a substantial release of both nitrogen and phosphorus compounds. These nutrients then flow down slope to the river. A riparian forest belt around the river protects it. Regarding water protection maintaining a strip of riparian forest is a must for near-river wood harvesting (Ahtiainen et al. 1999).

Riparian forests are a source of high biodiversity. It stems from two sources. Specialist species unique to riparian forests, or species rarely found elsewhere and generalist species found in upland as well as riparian forests. Some authors have found overall species richness to be higher in riparian rather than upland forests (Naiman et al. 1993) however on a larger scale the richness is similar (Sabo et al. 2005). This means α-diversity of the two types of forests is generally similar nevertheless β-diversity, i.e. a difference in species composition between these two forest types is constantly higher in riparian forests. Furthermore, the displacement of species from riparian to upland zones was stronger for plants than animals and stronger in dry than wet climates which can be explained by the fact that animals are mobile and that drier climate presents more extreme physical gradients like temperature and water availability (Sabo et al. 2005). Riparian forests thus support landscape connectivity and may act as reservoirs for forest generalist species (Gundersen et al. 2010).

1.4 Riparian forest dynamics

The dynamics of riparian forests could in simple terms be described as such: Newly emergent ground available for colonization by vascular plants is colonized by pioneer plants characterized by fast growth and rapid seed dispersal. Pioneer plants prepare the soil for non-pioneer plants as mentioned above. Later successional species fully overgrow the previous and create a canopy, shading the understory and the entire system is relatively stable until it is fully reset by another disturbance. In most cases this disturbance is abiotic for example flooding (Gonzáles et al. 2010). In recent years extreme anthropogenic disturbances occur in a form of a clear-cut or such as mentioned bellow (Bengtsson et al. 2000).

As flooding has such tremendous effect on the riparian dynamics and species composition (Kozlowski 2002, Turner et al. 2004), making research into this system is very important. The consequence of floods is a disturbance which is defined by White et Pickett (1985) as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. The strength of flooding changes both laterally and longitudinally within the river corridor. There is a clear trend of decreased water availability further the stand is from the active channel; on a longitudinal scale there is variation. While the strength of the current generally increases further the river flows and so does the flood strength the flow may also peak according to the river geomorphology (Lite et al. 2005).

Water is not only destructive for plants but also provides many important functions such as delivering nutrients, restoring groundwater levels and moving propagules (Bendix et Hupp 2000).

Heterogeneity generated by flooding disturbance is largely responsible for species diversity in alluvial areas (Lite et al. 2005, Pausas et Austin 2001). Plants adapt themselves to the flooding regime. Many woody species have the ability to resprout from roots thus the disturbance is not lethal for the individual (Bond et Midgley 2001). In addition to this effective strategy some species are dependent on disturbance to germinate from seeds on newly uncovered ground. These however suffer from river regulations and it is necessary for them to always have mature seed bearing populations. Lack of new regeneration opportunities compared to senescent stands being succeeded by other plants could seriously threaten the species (Stella et al. 2011, 2012).

While water is a principal resource in alluvial areas light availability also plays an important part especially in forests where trees create shade for understory herbaceous plants. Light has two effects on vegetation. It is needed for photosynthesis and thus crucial for plant growth. On the other hand energy from light demands evaporation and could potentially induce water stress (Pausas et Austin 2001). Streng (1986) has discovered that water conditions determine germination and survival of trees in the first few years. Later on, however, light conditions dictated survival. Also shade-tolerant species are able to survive floods if they have a lot of light radiation available but both shade and flooding at once are too stressful to survive.

It is important to mention invasive species when dealing with disturbances. Disturbances increase susceptibility to invasive neophytes (Pysek et Prach 1994). Also Hood et Naiman (2000) conclude that frequently flooded active channel floors are more invasible than channel banks.

1.5 Riparian forest management

Land use is one of the most important factors influencing species diversity globally in the past few decades (Hansen et al. 2004, Plue et al. 2008, Sala 2000). Thus it is an important research subject. Previously, forestry had one interest in mind: timber harvesting and forest management were done in light of such interest (Thomas et al. 1999). Recent social events force foresters to take species diversity into consideration. Social pressure to ecologically sounder management resulted in foresters shifting their official interest statement (Roberts et Gilliam 1995).

Natural protection is now primarily based in reserves. While investigators recognize their importance the effect of such areas can be lowered by poor management in adjacent non-protected land (Kintz et al. 2006). At the same time even with proper land use balancing both ecological and economical needs certain elements of natural forests are impossible to simulate. That is why reserves are crucial for maintaining biodiversity on a larger scale (Roberts et Gilliam 1995). Thus synergy of proper management in both reserves and timber harvest forests are a requisite for maintaining full biodiversity (Bengtsson et al. 2000).

In order to properly devise management for forested areas we need to first create a reference or a goal towards which we aim. Forests, especially riparian ones, are so dynamic in nature (Elliott et al. 1997) that researchers have dropped the term reference state rather choosing a more proper term reference dynamic (Boon et al. 1992). Dufour et Piégay (2009) state that historical reference dynamic might not be necessarily best for reaching full benefit for and from the ecosystem. However it seems reasonable to consider evolutionary history of plant species in forests to devise good management practice.

Throughout their evolutionary history forest plants had to adapt to abiotic as well as biotic disturbances. First megaherbivores caused severe but unselective grazing pressure onto plants (Owen-Smith 1987). Later on smaller herbivores took their place and applied a more selective but less severe grazing (but see Birks et al. 2005). Both of these grazing disturbances created open glades with few old trees (Nilsson 1997). In a history-based reference dynamics it is important to simulate these disturbances as a part of a proper management strategy (Bengtsson et al. 2000). Such management should lead to highest species diversity (Roberts et Gilliam 1995).

Coppicing and wood-pastures were among widely used forest management types for the past few centuries, however now their use is declining (Bergmeier et al. 2010). Coppicing, the act of cutting the trees close to the ground and letting them resprout, seems to have positive effects for example allowing oak stand regeneration (Altman et al. 2013). Furthermore periodically increasing light availability and site heterogeneity by coppicing allows for higher species diversity compared to homogenous plantations (Gondard et al. 2001). However, after coppicing is abandoned the stands naturally grow into a homogenous low-diversity state (Nagaike et al.2003), thus continually maintaining proper management is important.

Similarly, forest pasture, i. e. letting animals like deer or sheep graze in the woodland, widens the wood to grassland ecotone thus locally increasing biodiversity (Bergmeier et al. 2010). The presence of ungulates affects the forests in a plethora of ways from grazing and bark removal to trampling and depositing nutrients, this influences various woody species dynamics (Danell et al. 2003).

Nowadays a widespread type of land use is called clear-cutting. It is a local unselective felling of the entire canopy. Such disturbance is quite extreme and foresters sometimes compare it to abiotic factors such as flooding of windfall. Such comparison is misleading as clear-cutting lacks certain crucial element such as leftover dead wood (Niemelä 1997).

It is common for groundwater levels to increase after clear-cutting due to limited evapotranspiration (Perison 1997). However Sun et al. (2001) discovered that groundwater levels stabilize in the second year after clear-cut as the regrown herbaceous layer re-establishes evapotranspiration yet hydrology could still be affected by changing soil physical properties. Resources such as light become more available after clear-cut changing species composition towards the shade-intolerant end of the spectrum promoting growth of herbs and shrubs (Fredericksen et al. 1999).

Another common forestry practice is site preparation in form of ploughing or fertilizing. These generally have a substantial effect on vegetation (Roberts et Gilliam 1995). A study by Libus et al. (2010) has shown that ploughing can help the invasion of a neophyte *Aster lanceolatus* to alluvial areas.

As forestry intentions shift so does the management and newer options are unveiled (Malcolm et al. 1995). A less invasive approach is thinning or selective harvest. While it allows timber harvesting it also opens up the canopy letting more light in. However it is not as extreme as clear-cut. More light for the herbaceous layer means more cover and biomass and thus theoretically higher species biodiversity (Stone et Wolfe 1996). However, the data is inconclusive as thinning creates physical disturbance in form of trampling during harvest. It is still an ecologically sounder land use (Thomas et al. 1999).

The method of green tree retention where a few trees are left on the stand to simulate pre-harvest conditions has shown some positive effect (Malcolm et al. 1995, Halpern et al. 2005). A new study pronounces the benefits of green tree retention in riparian forests suggesting that local vegetation is more resistant to moderate harvest induced disturbance and changes little thereafter (Zenner et al. 2013).

As shown above riparian forests are an important and endangered part of our landscape. We draw many benefits from them and in order to manage them sustainably we need to understand the dynamics properly and evaluate the effect of various land uses. Therefore this thesis sets up for two goals:

1) to analyze riparian forest vegetation and correlate it along light and moisture gradient
2) find out how different management techniques affect plant diversity.

2. Study area

2.1 Location

The study area is located in South Moravia in the Czech Republic (Central Europe). It is a series of alluvial meadows and woodland along rivers Dyje (Thaya) and Morava (March) spanning across 146 km^2 ha of area. The southern tip of the study area is at the confluence of the two rivers at 149 m. a. s. l. About 30% of all riparian forests of the Czech Republic are within this area (Vybíral 1996).

The study area is a biodiversity hot spot for various taxa (Vicherek et al. 2000). Local mean annual temperature and precipitation is 9.6˚C and 500 mm respectively (Miklín et Čížek 2013).

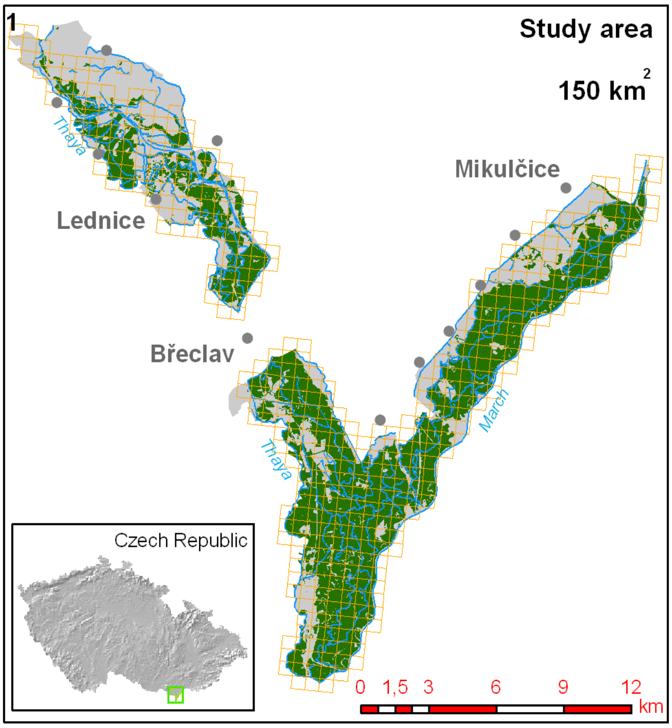

Fig. 1: Study area in South Moravia with forested area highlighted by green color.

2.2 Forest history

About 12 thousand years ago wind conditions started shaping the area creating sand dunes called "Hrúdy" in this thesis further referred to as hummocks (Havlíček 2004). These hummocks were up to 8 meters higher than the surrounding area. Their creation was possible due to a lack of high-standing vegetation blocking the wind. Warming about 9 thousand years ago made the area wetter resulting into afforestation by hardwood species like oaks, elms or maples.

With the warmer climate human settlers colonized the area mostly building their settlement on hummocks due to their drier conditions. Human effects intensified some 5 to 7 thousand years ago due to first agriculture (Miklín et al. 2010). Settlers maintained deforested areas and open canopy pasture forests. Forests were also used as a source of firewood via coppicing.

Settlers of the emerging Great Moravian Empire around the 8th century shaped the location further by more deforestation resulting in minimizing altitudinal differences throughout the area via stronger floods (Miklín et al. 2010). This change of water conditions shifted species composition towards softwood species like willows or poplars (Grulich 1992).

Due to increased demand for wood during the industrial revolution pasturing in forests was forbidden in 1754. The ban was disregarded by the peasants till 1873 when the Liechtenstein dynasty used military force to drive the local villagers from the forest which is recognized as the advent of organized forestry in the area (Nožička 1956).

2.3 Current forest situation

With pasture in forests banned, the once open forests closed. New exotics species such as *Juglans nigra* were introduced (Nožička 1956). Now the majority of stands are homogenous close forests (doubled their area in the last 70 years) and other forest types, while once abundant, declined drastically (Miklín et Čížek 2013). Currently the forest is managed by forest company Židlochovice under Forests of the Czech Republic. Wood extraction is done by clear-cuts of up to 2 ha area while planting oak (*Quercus robur*) and ash (*Fraxinus angustifolia subs. danubinalis*) with 140/110 year rotation (Miklín et Čížek 2013).

Water conditions were also seriously affected by alterations of river flow finishing with construction of The Nové Mlýny reservoirs during late 20th century. The Nové Mlýny reservoirs are a cascade of three reservoirs amounting to the second largest water body in the Czech Republic. This caused irreversible damage to riparian ecosystems and limited floods. Locals later tried to restore the flood regime artificially starting in 1992 (Pražák et Kloupar 1996). The restoration was fairly successful but could not fully simulate historical conditions.

2.4 Botanical richness

While the area is alluvial the hummock occasionally rising among the flatland provide a mosaic of drier conditions. Among the most abundant woody species are pedunculate oak (*Quercus robur*), narrow-leaved ash (*Fraxinus angustifolia subs. danubinalis*) representing dominant hardwood species. On more water-logged areas poplars (such as *Populus alba*) and willows (such as *Salix alba*) are present. Field maple (*Acer campestre*) forms dense shrubs.

Herbaceous species common in forested areas are for example various sedges (*Carex riparia*, *C. sylvatica*), grasses (*Phalaris arundinacea*), summer snowflake (*Leucojum aestivum*) abundant here yet rare elsewhere in the Czech Republic, or the endangered Hungarian iris (*Iris variegata*) bound to the drier hummocks. Alluvial meadows are also very species rich being home to a plethora of endangered species (Fillipov 2007) such as angle onion (*Allium angulosum*), spear-leaved skullcap (*Scutellaria hastifolia*), or Siberian iris (*Iris sibirica*). Among water vegetation the nettle *Urtica kioviensis* can only be found here in the entire Czech Republic (Danihelka et Lepší 2004). Apart from rare species, incorrect management supports invasions of panicled aster (*Aster lanceolatus*) invading both prepared forest clearings and unmown alluvial meadows (Fillipov 2007). Panicled aster alongside Hymalaian balsam (*Impatiens glandulifera*) and devil´s beggar-ticks (*Bidens frondosa*) also invade regulated river banks pushing out native flora (Fillipov 2007).

3. Methods

3.1 Data collection

The analysis is based on phytocenological data recorded on 297 plots. Each plot is based on a 100 m^2 area centered on a marked tree or stump. Data was gathered twice for each plot to encompass both spring and summer aspect. The spring aspect was collected in mid-April of 2012. The summer aspect was collected in the beginning of July 2012.

A percentage of cover was recorded for three layers: **E1** (herb/juvenile layer < 1 m, **E2** (shrub layer 1-5 m) and **E3** (tree layer > 5 m). Plant species were then recorded within their according layer so that one species could potentially be in all three layers. Herbaceous plants were always occupying E1 regardless of their height. Each species were designated cover in the respective layer using the Braun-Blanquet scale with 2 divided (Braun-Blanquet 1964): **r** = < 0,1%; **+** = 0,1 – 1%; **1** = 2 – 5%; **2m** = 5 – 10%; **2a** = 10 – 15%; **2b** = 15 – 25%; **3** = 25 – 50%; **4** = 50 – 75%; **5** = 75-100%. When a species is present in both aspects the higher cover value is kept. Vegetation data was digitalized using Turboveg v. 2.98a (Hennekens et Schaminee 2001). Data check was done in Juice 7.0 (Tichý 2002).

Each plot was classified in one of three categories: **Hummock** (driest, locally called hrúdy, refer to Chapter 2), **Flatland** and **Swamp** to show the level of moisture availability. To measure light availability each site had canopy cover estimated. Management types were divided into 7 categories. Specified categories are as follows: **Tree line, Clearing, Plantation, Solitary tree, Coppice, Forest pasture** and **Coppice with standards**. It is important to say that neither forest pasture nor coppicing is practiced within the study area today and has not been for some time (see Chapter. 2). Therefore the last three categories have only been managed in such way historically.

To measure current land cover (LC), area of 8 types of LC was estimated in a circle centered at the plot with 60m radius. Omitting the central part with 5m radius, three ring segments of this circle were used in the analysis: 5-15m; 15-30m and 30-60m in radius. LC types used are: **Forest, Young forest, Clearing, Tree line, Water, Forested swamp, Meadow** and **Field**.

Each species was labeled with one of three residence time statuses: **Native, Archaeophyte** and **Neophyte**. Then each species was also labeled with one of four invasive statuses: **Native, Casual, Naturalized** and **Invasive**. Both status types were obtained from The Checklist of vascular plants of the Czech Republic (Danihelka et al. 2012). Species were then coupled according to their status and cover in m^2 was summed among every status for comparison.

3.2 Data analysis

To analyze effects of moisture and management on total and E1 (herbaceous/juvenile) species richness, four One-Way ANOVAs (Analysis of Variance) were executed each with one explanatory variable and one type of species richness.

Furthermore several ANOVAs were used to analyze effects of management types on cover taken up by species according to their residence time and invasive status. Two complementary ANOVAs testing the dependence of invasive species count relative to total and E1 species on management were also performed.Tukey range test was also performed for all ANOVAs to show distinctions between individual explanatory variable types. Results are presented where appropriate.

Regarding multivariate methods, first a DCA (Detrended component analysis) with canopy cover, humidity and management type as supplementary variables was executed to explore species diversity among plots. Shannon-Wiener species diversity index (Whittaker 1972):

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

was used to supplement simple numerical species diversity.

To analyze the effect of environmental variables on species composition, four constrained analyses were performed: 1) CCA (canonical correspondence analysis) with cover, humidity and management as explanatory variables. 2) Partial-CCA with management as the explanatory variable using humidity as the covariate. Canopy cover was not used as a covariate because of its inherent connection to management and using it might have partitioned out viable variation explained by management. 3) CCA for the three closest types: plantation, pasture forest and coppice with standards. Only the management type was used as an explanatory variable. 4) For comparison variation partitioning testing simple effects of both management and moisture was executed for the three abovementioned management types.

A set of three CCAs was used to analyze the effect of current land cover on species composition in the three ring segments specified above.

To show how management types alter species composition in regards to their invasive and residence type statuses, two RDA´s (redundancy analysis) were executed.

All univariate methods with their visualization were done in Statistica 8 (StatSoft 2011). All multivariate analyses and visualizations were done in Canoco 5 (ter Braak et

Šmilauer 2012) and all used Monte-Carlo permutation tests to calculate significance using 999 permutations.

4. Results

4.1 Univariate analyses of environmantal variables

There are no significant differences among moisture types for both total species richness (**F=2.27; DF=2, 294; p=0.105**) and E1 (herbaceous/juvenile) species richness (**F=2.57; DF=2, 294; p=0.077**). Yet significance fairly close to the 5% margin warrants graphical exploration.

Regarding moisture conditions, the results show that hummocks have slightly higher E1 species diversity (both in median and 3rd quartile) while swamps and flatland host similar diversity (Fig. 2).

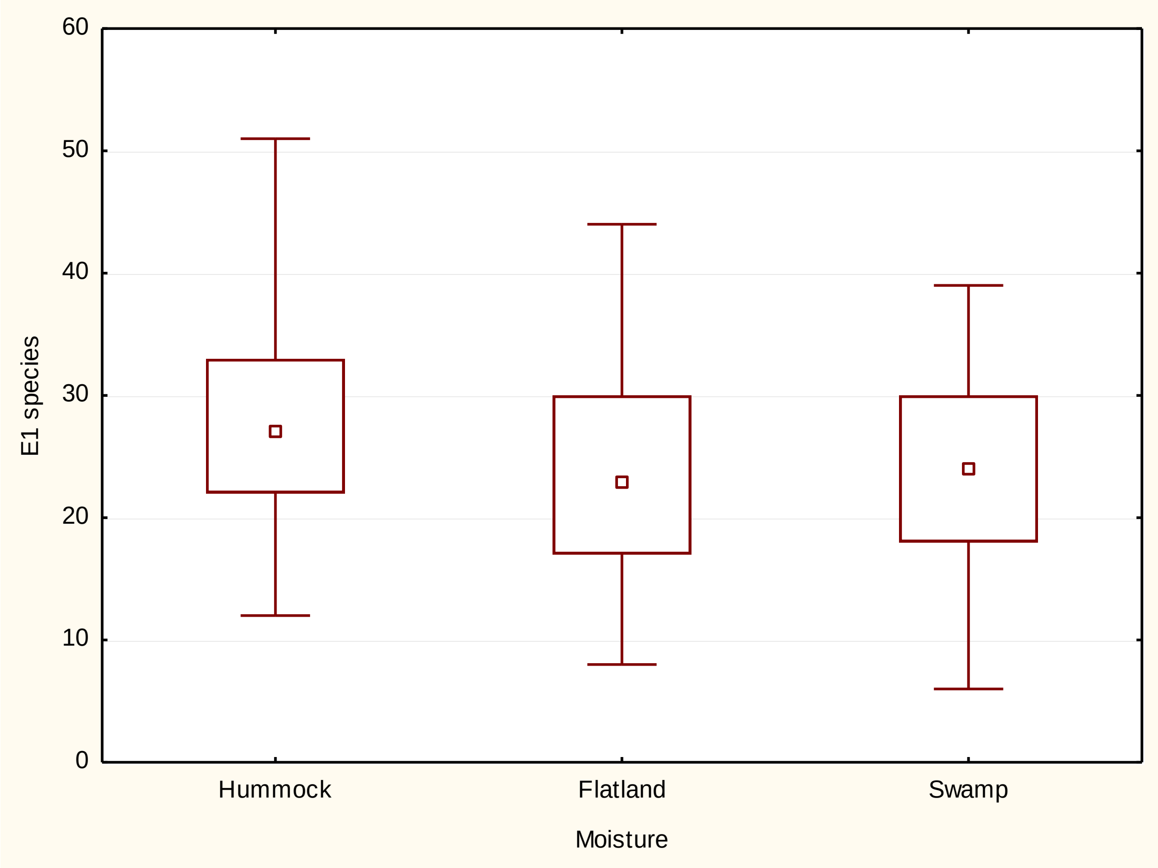

Figure 2: Dependence of E1 (herbaceous/juvenile) species richness on the three moisture levels. Hummock slightly differs from the rest with highest richness. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

Unlike moisture conditions, there are significant differences among management types for both total species richness (**F=10.540; DF=6, 290; p<0.001**) and E1 species richness (**F=11.807; DF=6, 290; p<0.001**).

Regarding both total and E1 species richness, clearing and solitary trees are the richest while plantations, pasture forests and coppices with standards are the lowest (Fig. 3, 4). Both clearings and solitary trees are significantly different form all three of plantations, pasture forests and coppices with standards in total species richness.

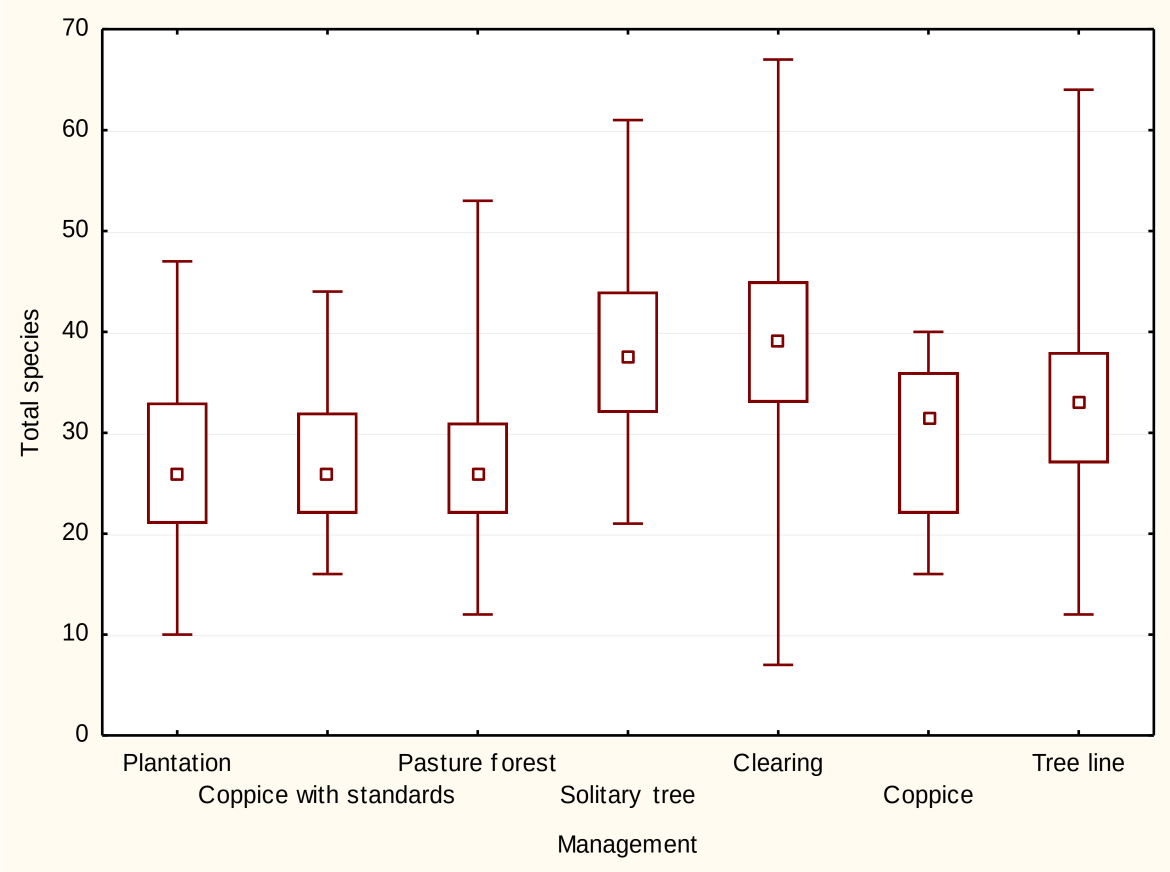

Figure 3: Dependence of total species richness on management type. Clearing and solitary trees are highest while plantations, pasture forests and coppices with standards are the poorest. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

Considering E1 species richness, tree lines are slightly richer and solitary trees slightly poorer (Fig. 4). In addition, clearing are also significantly different (**Between MS=83. 188; DF=260; p=0.024**) from tree lines.

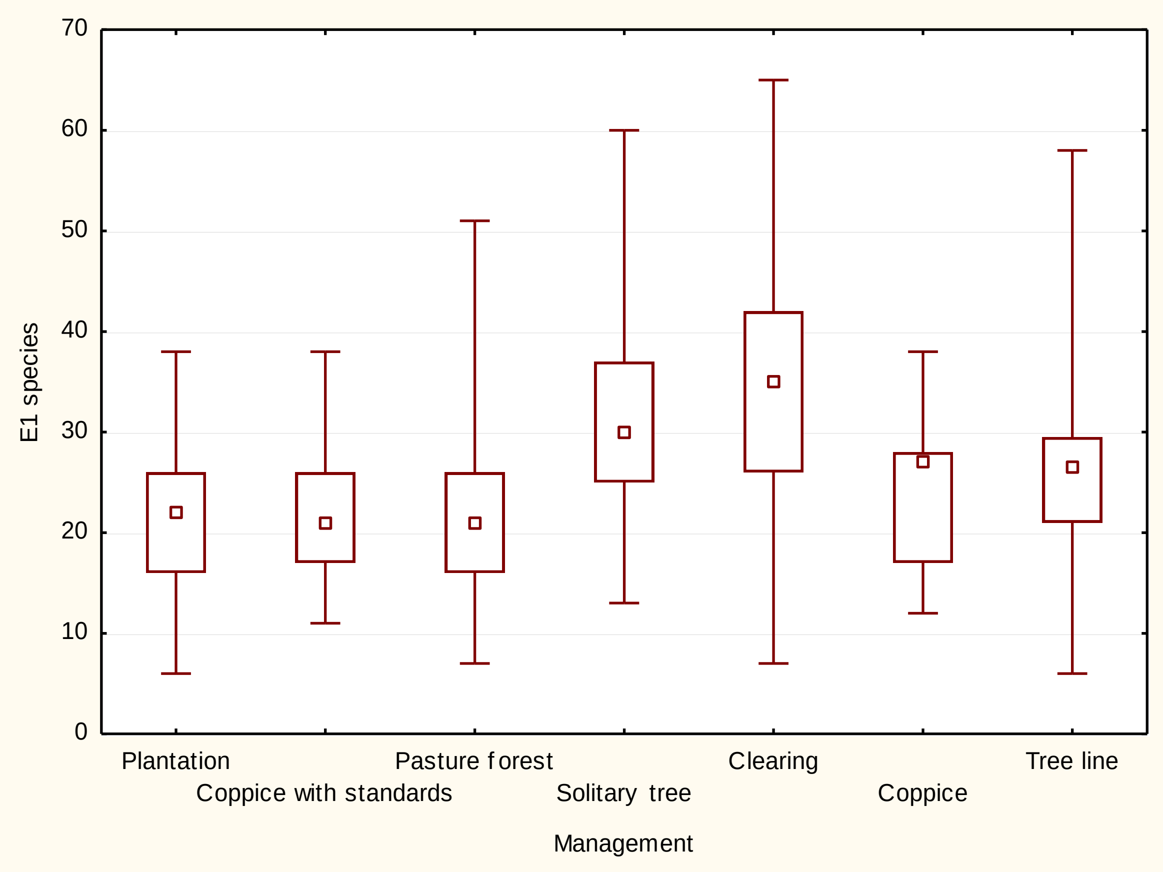

Figure 4: Dependence of E1 species richness on management type. Clearing have the highest richness with solitary trees slightly behind. Plantations, pasture forests and coppices with standards are the poorest. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

4.2 Species diversity exploration

A total of 408 species were found in all plots. The three most abundant herbaceous species were *Ficaria verna subs. bulbifera* (present on 265 stands), *Rubus caesius* (243) and *Urtica dioica* (222). Alarming is the abundant presence of invasive species *Impatiens parviflora* (149) and *Aster lanceolatus* (114).

DCA for the species composition data shows that the first two unconstrained axes explain **3.87%** and **7.01%** of variability cumulatively.

Shannon-Wiener index measuring diversity suggests that solitary trees are the richest (Fig. 5). Clearings and tree lines follow, with the rest close by regarding their diversity. Cover is negatively correlated with species diversity and hummock is the most diverse moisture type.

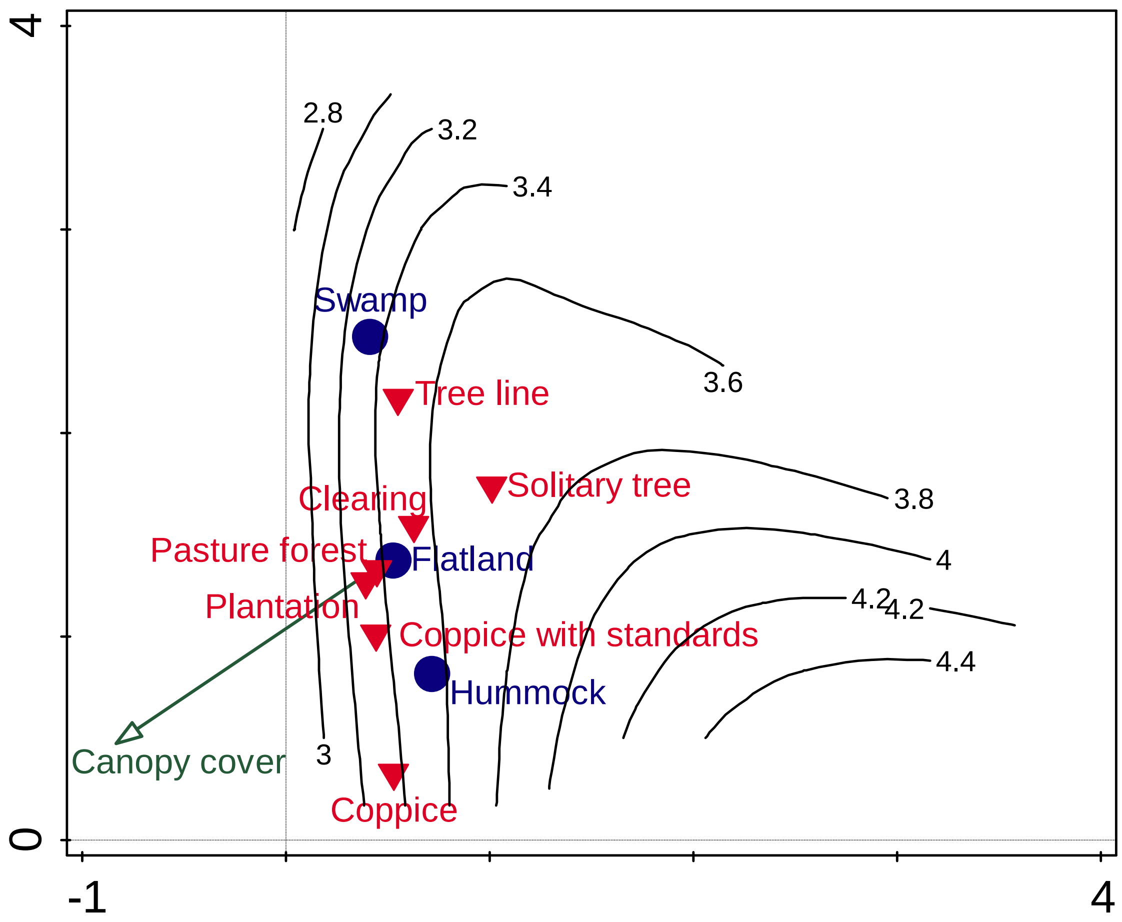

Figure 5: Contour plot, resulting from DCA, showing the dependence of species diversity, expressed by the Shannon-Wiener index, on passively projected moisture, canopy cover and management type. Solitary trees are the richest.

4.3 Effect of environmental variables and land cover on species composition

Monte-Carlo permutation test for the performed CCA with canopy cover, moisture and management as explanatory variables shows significant differences on all axes **(pseudo-F=2.5; DF=9; p=0.001 at 999 permutations)**. Explanatory variables account for 7.3% of variance. First and second axes explain 1.98 and 3.49% cumulatively. Solitary trees, tree lines and coppices are far away from the rest in the ordination space (Fig. 6). Pasture forests, plantations and coppices with standards are very similar. Clearings and solitary trees are negatively correlated with canopy cover. All three moisture types are dissimilar.

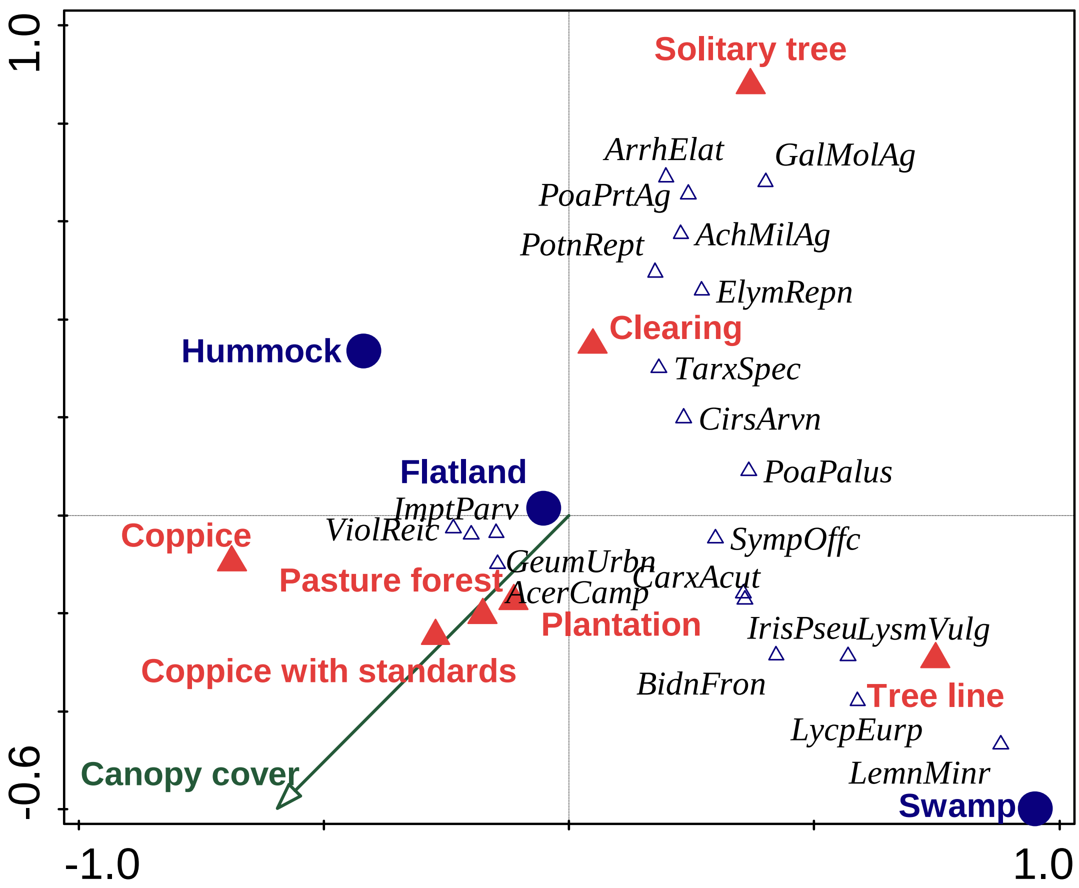

Figure 6: Ordination diagram resulting from CCA summarizing the dependence of twenty best-fitting species (woody species have number before name corresponding to the vegetation layer, no number means juveniles) on the three explanatory variables (management type; moisture and canopy cover).

Monte-Carlo test for partial-CCA with moisture as a covariate shows significant differences between various management types on all axes **(pseudo-F=2.1; DF=6, 2; p=0.001 at 999 perm.)**. After filtering out the effect of water conditions, management still accounts for 4.3% of variance. Filtering out the covariate increases the distinction of clearings from the rest (Fig. 7). Solitary trees still remain different.

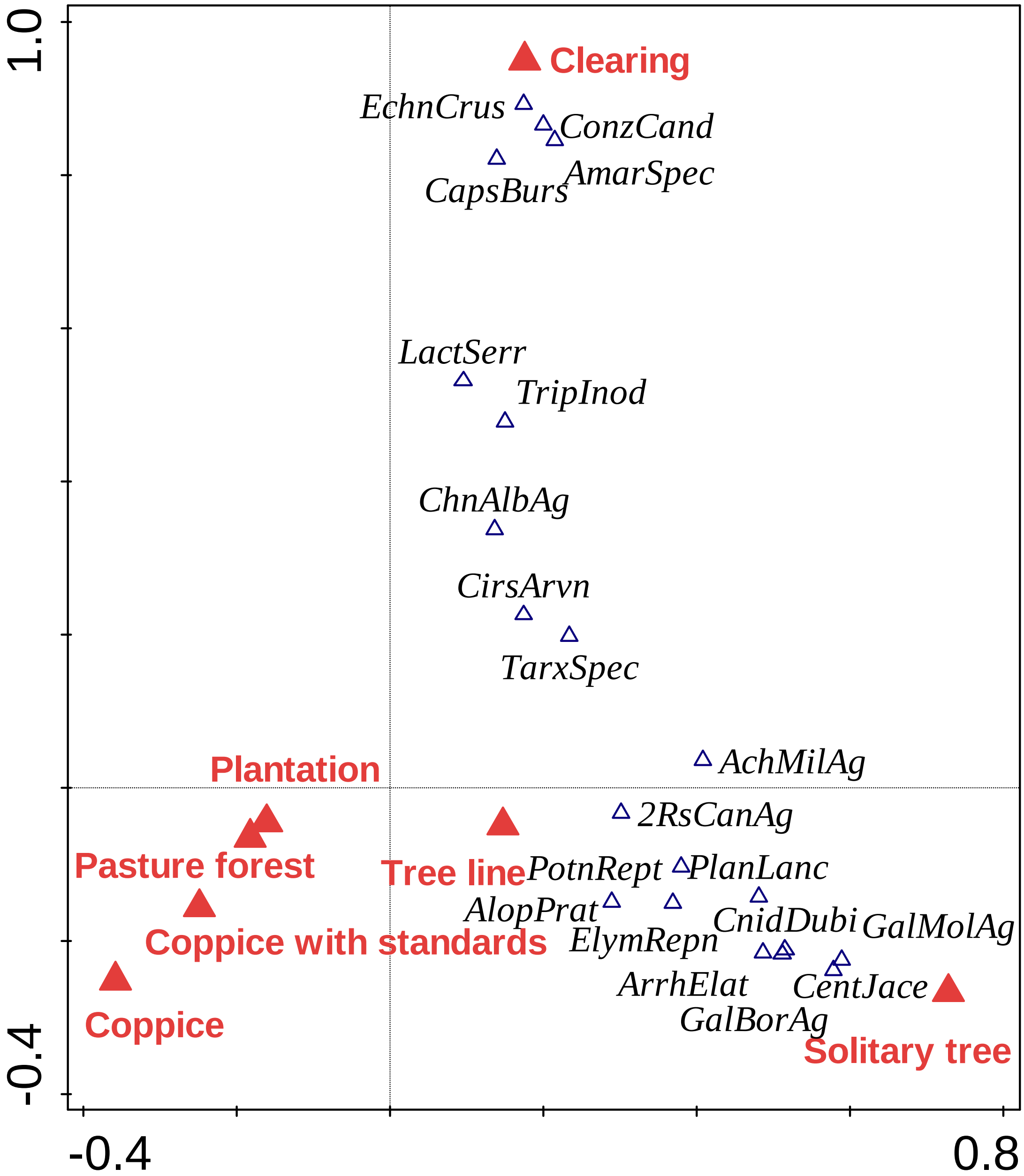

Figure 7: Ordination diagram resulting from partial-CCA with moisture conditions as a covariate to management type as the explanatory variable. The dependence of twenty best-fitting species (woody species have number before name corresponding to the vegetation layer, no number means juveniles) to the seven management types is summed up here. For comparison without the covariate refer to Fig. 6.

As both Fig. 6 and 7 show close relation of plantations, pasture forests and coppices with standards, further analysis is tried to show distinction. Monte-Carlo permutation test shows significant differences among plots belonging to one of three categories: plantations, pasture forests and coppices with standards (**pseudo-F=1.3; DF=2; p=0.005 at 999 perm.**). Management itself explains 1.3% of variation. Coppices with standards are further from pasture forests with plantations being between them (Fig. 8).

Variation partitioning shows that the shared effect of both management and moisture explains zero variance even though moisture itself explains 2.7% of all variation (**pseudo-F=3.8; DF=2; p=0.001 at 999 perm.)** Therefore moisture and management both explain different parts of variation having no shared explanatory power for the three management types tested in this analysis.

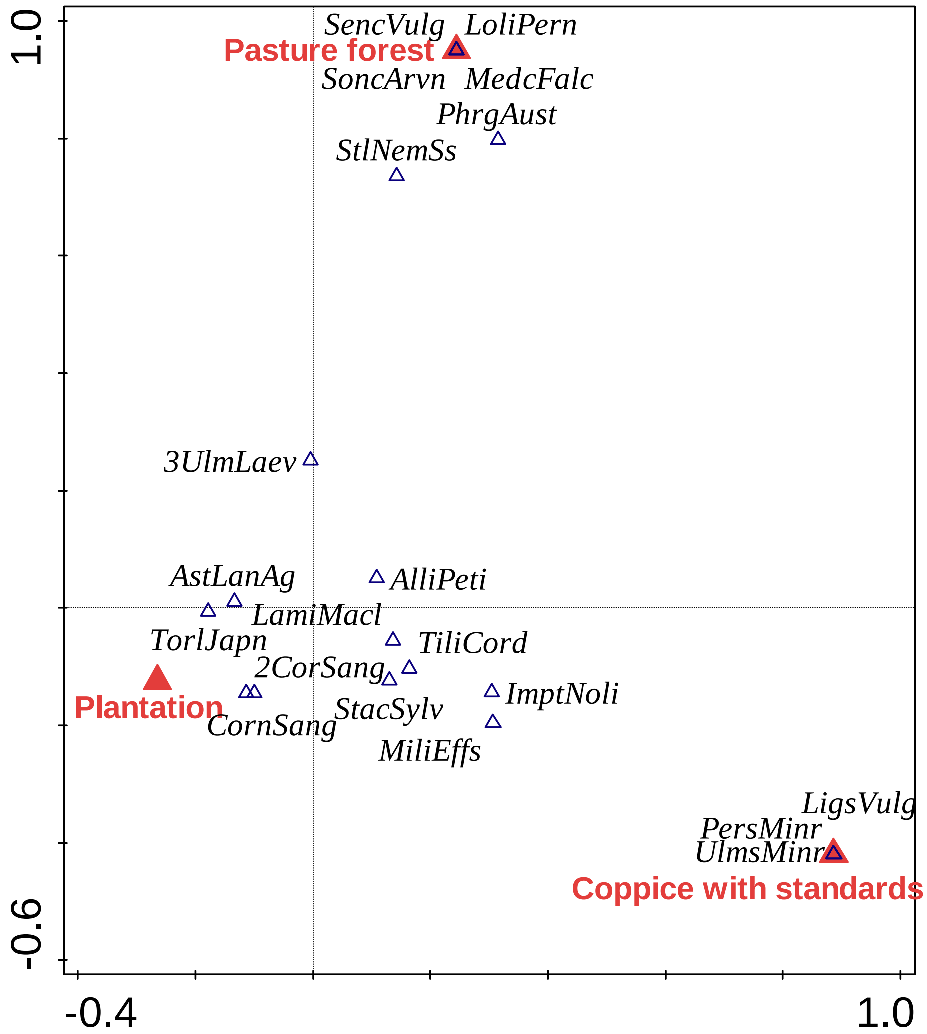

Figure 8: Ordination diagram resulting from CCA with management type as the explanatory variable. The dependence of twenty best-fitting species (woody species have number before name corresponding to the vegetation layer, no number suggests juveniles) to the three types selected to create a more detailed comparison than that which can be found in Fig. 7.

Monte-Carlo permutation tests for all three CCAs using land cover as variables for explaining species composition show significant differences among plots on all axes: **pseudo-F=2.5; DF=8; p=0.001** for the 5-15m ring segment explaining 6.5% of variance, **pseudo-F=2.6; DF=8; p=0.001** for the 15-30m ring segment explaining 6.7% and **pseudo-F=2.3; DF=8; p=0.001** for the 30-60m ring segment explaining 6.0% of variance. While the first two segments explain almost identical amounts of variance, the steady decline after the second segment suggests a possible decline in explanatory power further away from the plot center. To visualize land cover results the second segment (15 – 30m) is used due to its highest explanatory power. Forests as land cover type have the highest explanatory power with meadows being second (Fig. 9). Forests are also furthest away from the rest and are strongly negatively correlated with meadows. Overall, this shows that land cover can predict plant composition even far away from the actual plot.

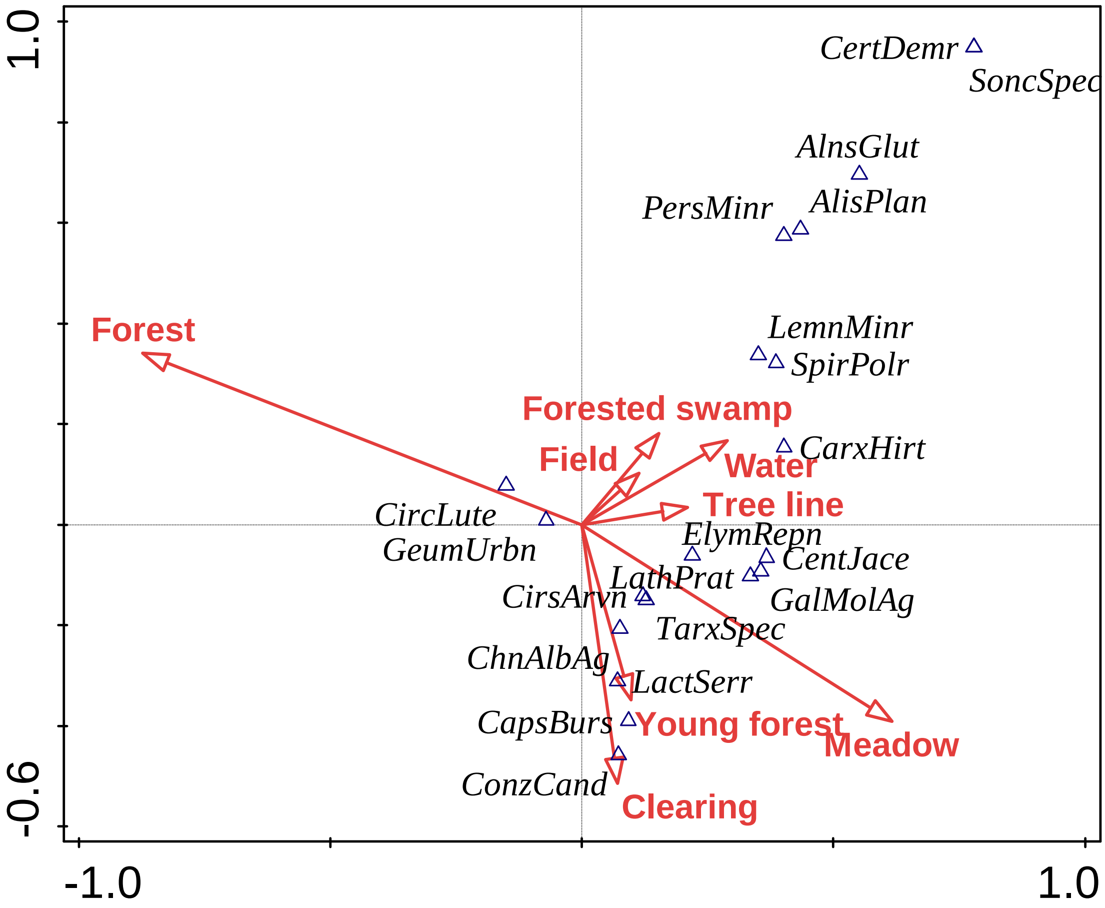

Figure 9: Ordination diagram resulting from CCA summarizing dependence of the twenty best-fitting species (woody species have number before name corresponding to the vegetation layer, no number means juveniles) on land cover in a ring segment of a circle from 15 to 30 meters from the plot center. Forests are furthest away from the rest while having the highest explanatory power.

4.4 Effects of management on species composition regarding invasive and residence time statuses

Total amount of neophyte and archaeophyte species found on all plots was 26 and 35 respectively. There were 3 casual, 38 naturalized and 20 invasive species. Invasive species are represented by 2 casuals, 5 archaeophytes and 19 neophytes. There are 347 native species.

Monte-Carlo permutation test for RDA using management types to explain species diversity in regards to residence times shows significant differences among all axes (**pseudo-F=7.5; DF=6; p=0.001 at 999 perm.**). Management types account for 13.5% of variation. Clear affinity of neophytes to plantations is in contrast to pasture forests, tree lines and coppices with standards being more abundant in native species (Fig. 10). Solitary trees and clearing correlate with archaeophytes.

There are significant differences between management types for neophyte (**F=2.791; DF=6, 290; p=0.012**), archaeophyte (**F=13.011; DF=6, 290; p<0.001**) and native (**F=7.228; DF=6, 290; p<0.001**) species cover.

Coppices have the highest cover of neophytes while solitary trees have the least (Fig. 11). These two types are also the only two significantly different (**Between MS=318.18; DF=290; p=0.011**)

Clearings and solitary trees have the highest cover of archaeophytes with the rest having little (Fig. 12). Clearings are also significantly different from all other management types. Solitary trees only differ from plantations, pasture forests and coppices with standards.

Coppices with standards have the highest cover of native species while clearing have the least (Fig. 13). Clearings are significantly different from all other management types.

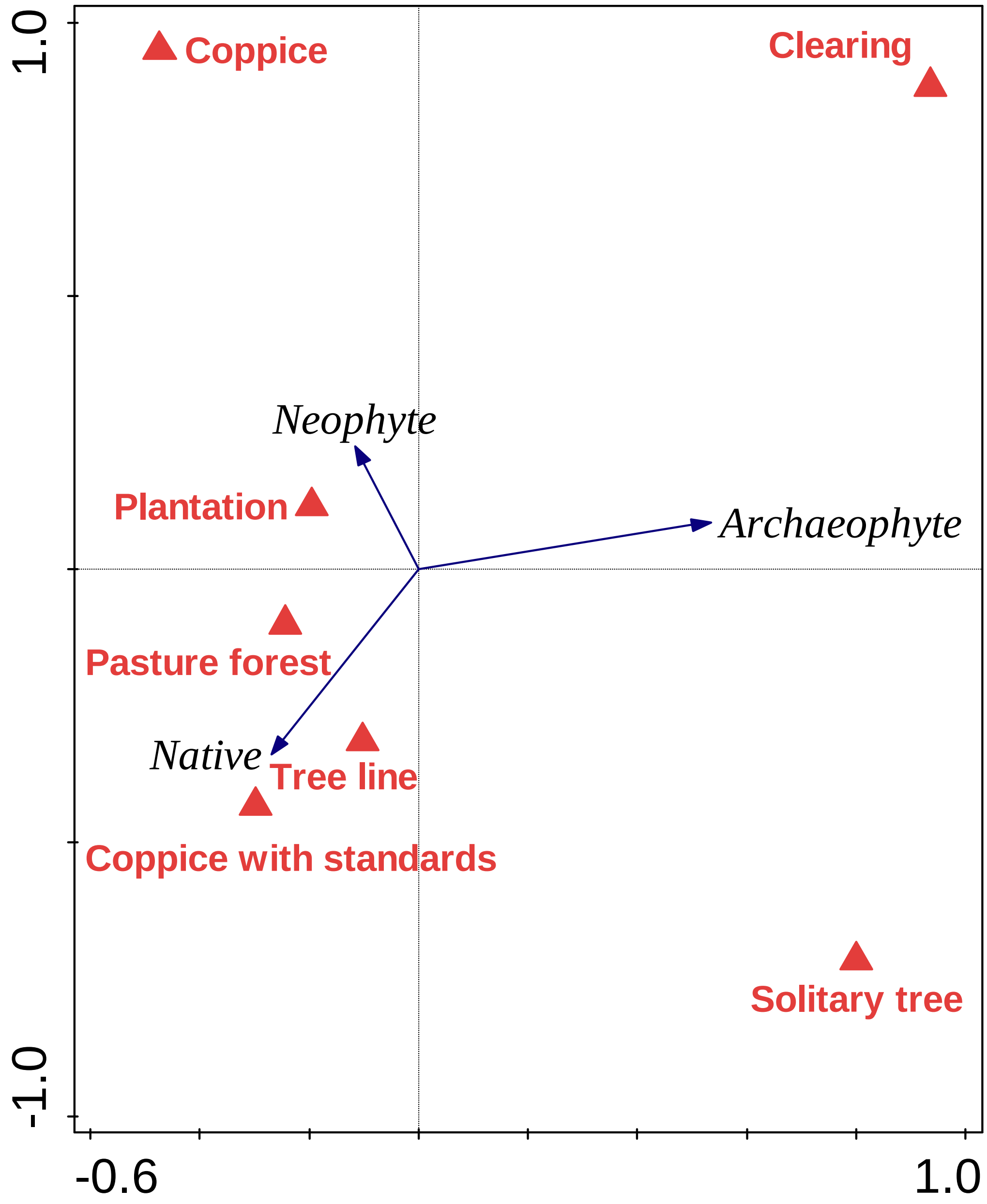

Figure 10: Ordination diagram resulting from RDA using management types to explain total cover of species summed by residence time statuses. Pasture forests, tree lines and coppices with standards correlate with native species in contrast to plantations and coppices closer related to neophytes.

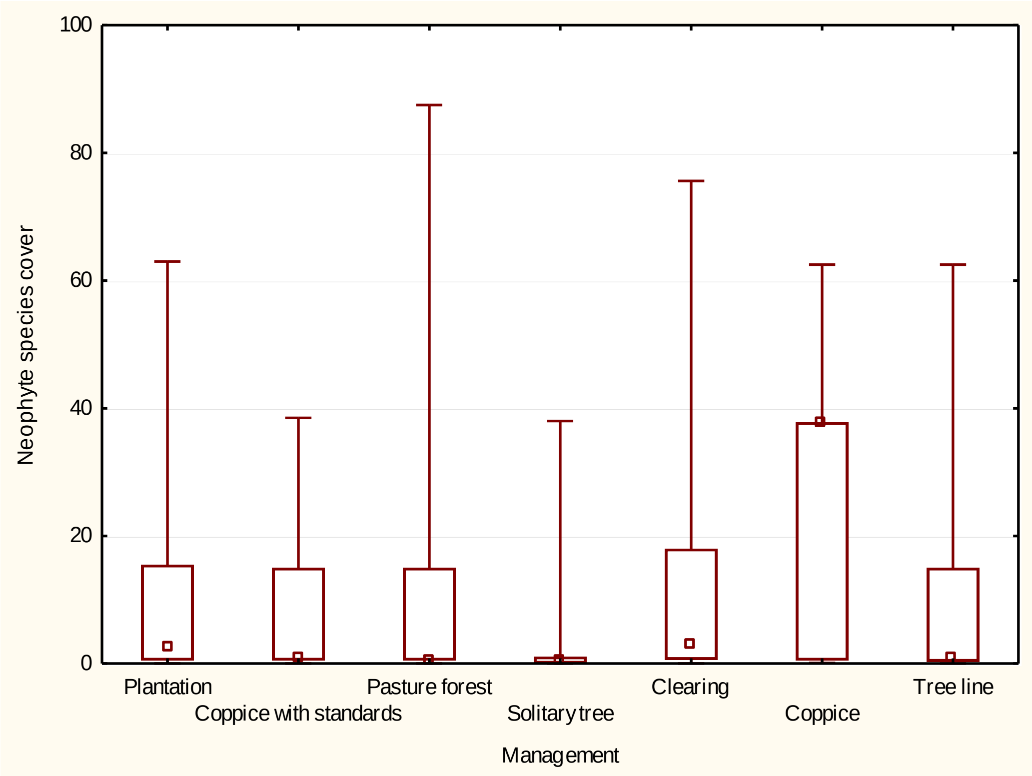

Figure 11: Dependence of neophyte species cover on management types. Coppices have the highest cover of neophytes. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

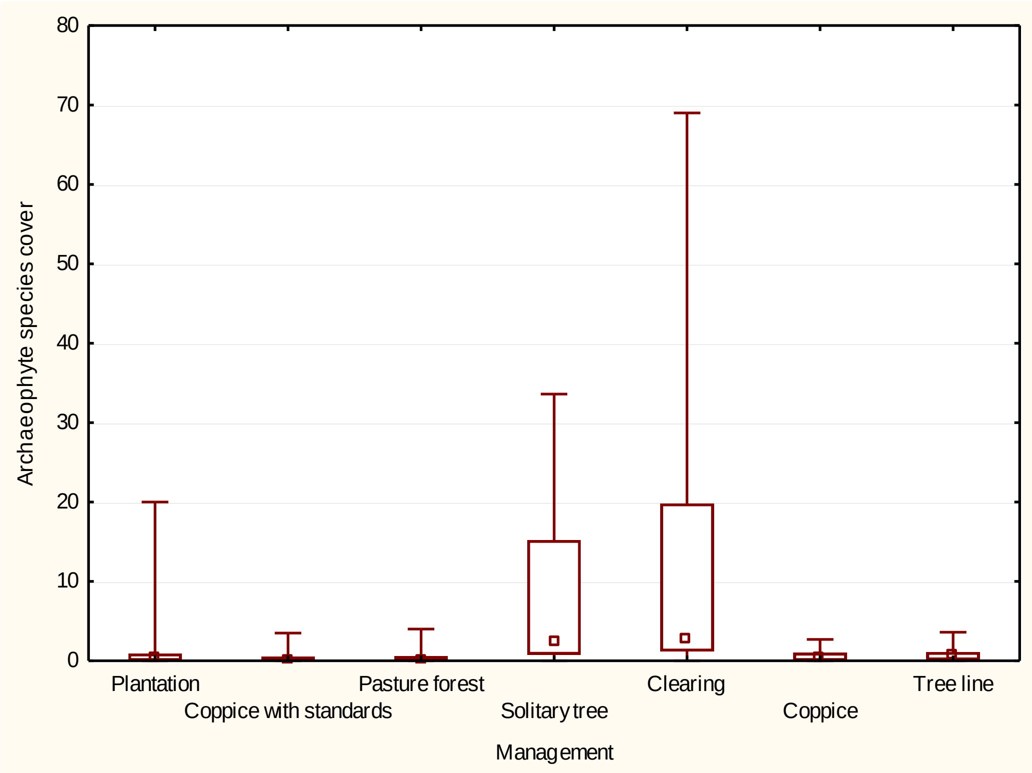

Figure 12: Dependence of archeophyte species cover on management types. Clearings and solitary trees have the highest cover of archaeophytes. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

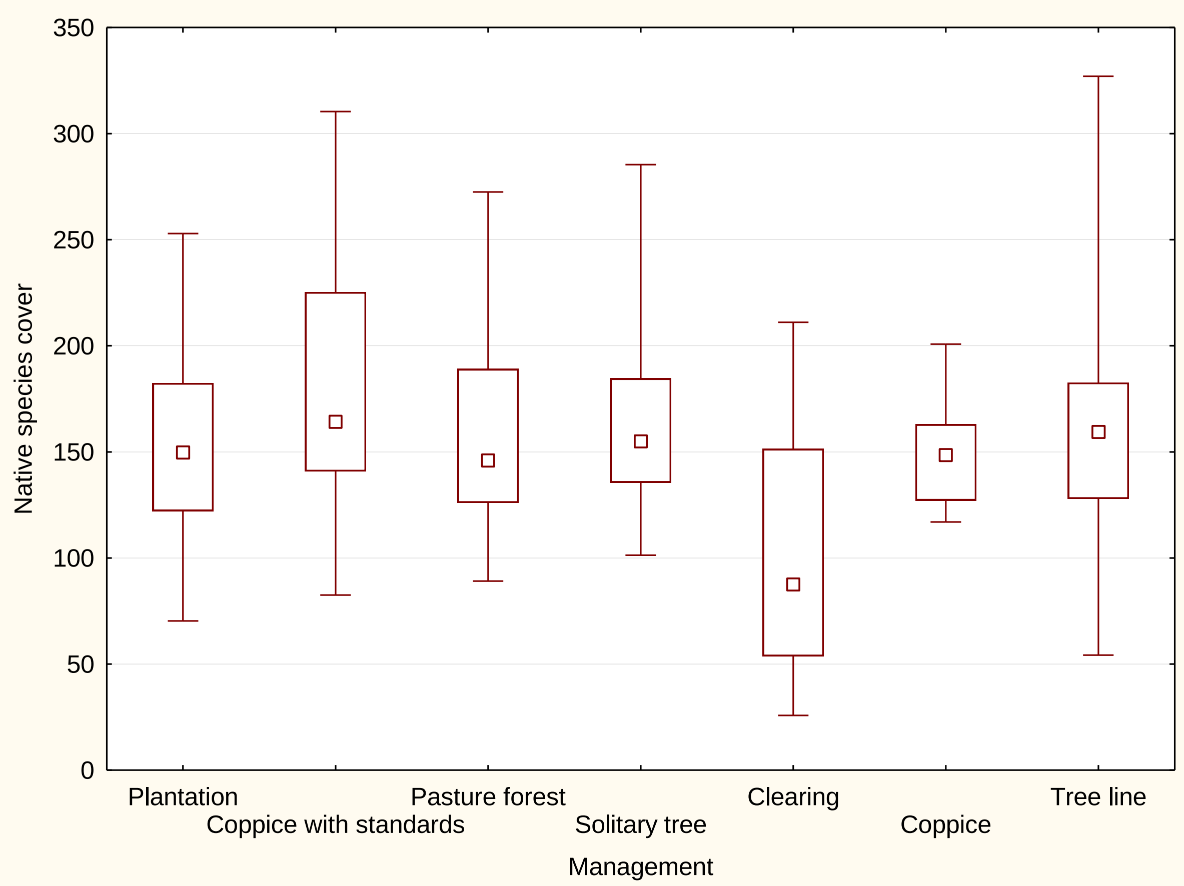

Figure 13: Dependence of native species cover on management types. Coppices with standards have the highest cover of native species. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

Monte-Carlo permutation test for RDA using management types to explain species diversity in regard to invasive status were also significant among all axes (**pseudo-F=3.7; DF=6; p=0.003**). The differences are smaller compared to the previous RDA yet management still accounts for 7% of variation. Casual types were few in numbers hence explain very little. Coppices with standards, tree line and pasture forests are close together with native species while plantations and coppices correlate with invasive species (Fig. 14). Naturalized species are best related with clearings.

Since there are very little naturalized neophytes and invasive archaeophytes, ANOVA results for invasive statuses are very similar with residence time analyses, hence only shown in the supplementary material.

To complement results from cover taken up by invasive species, ratio of invasive to total species count was also used. There are significant differences among management types in the ration of invasive species (**F=3.261; DF=6, 290; p=0.004**). Clearings have a very high ration compared to the rest (Fig. 15).

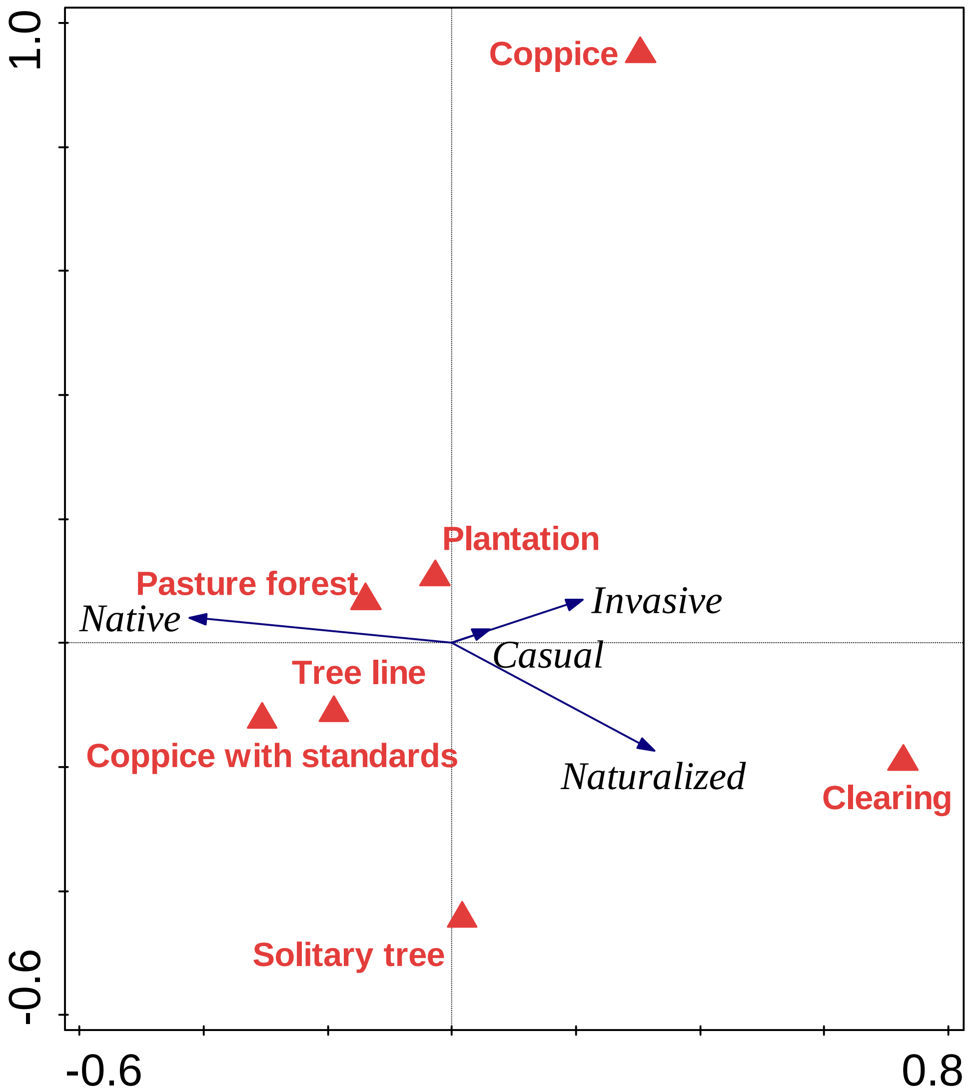

Figure 14: Ordination diagram resulting from RDA using management types to explain total cover of species summed by invasive statuses. Pasture forests, tree lines and coppices with standards correlate with native species in contrast to plantations and coppices closer related to invasive species.

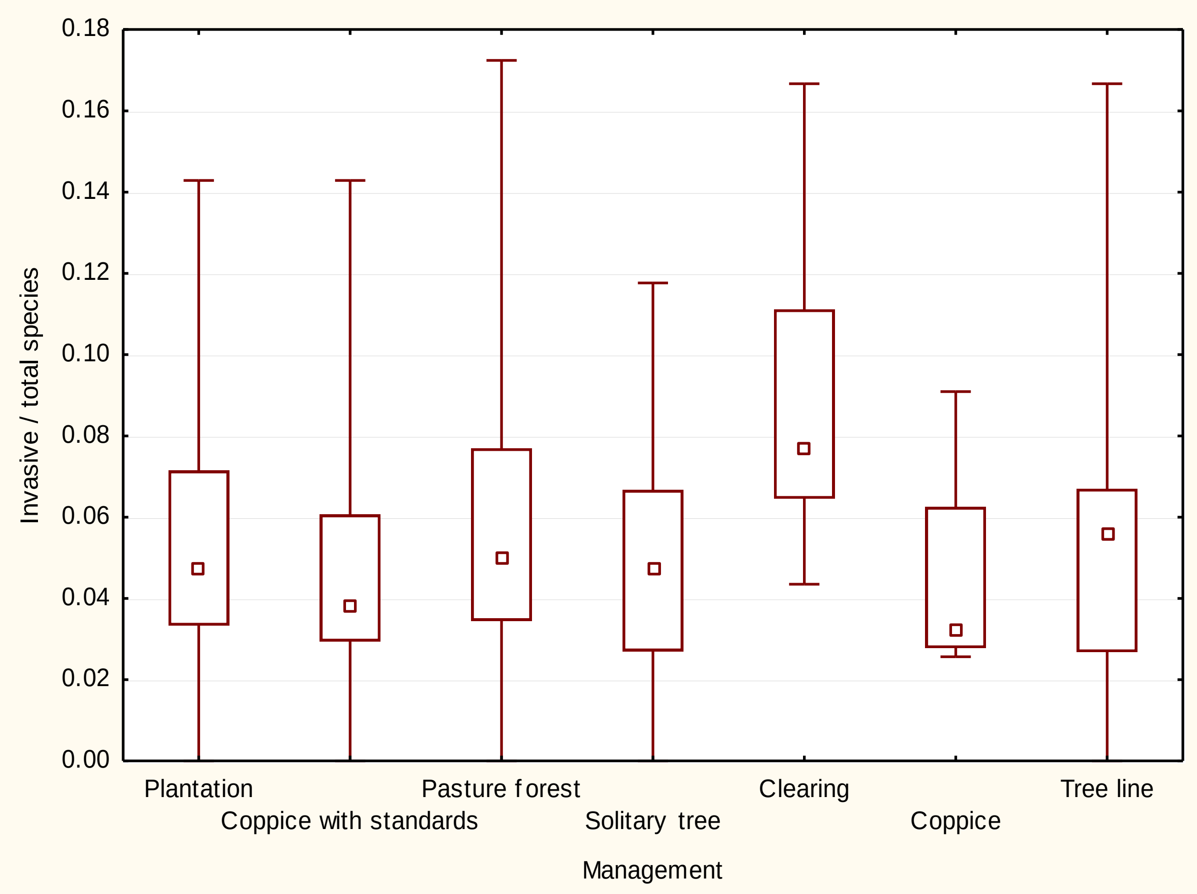

Figure 15: Dependence of the ratio of invasive to all species on management types. Clearing have the highest ratio. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

5. Discussion

5.1 Environmental effects on plant species richness

Water is an important factor in plant development and as such it affects species composition in many ways (Keddy et Ellis, 1984, Vervuren et al. 2003, Stella et al. 2011). Even for alluvial areas where lack of water may not be an important factor, water mediates disturbance affecting species composition (Lite et al. 2005, Pausas et Austin 2001). Flooded areas present an opposite kind of stress plants have to handle (Rood et al. 2010).

Some 12 thousand years ago, wind swept the study area creating sand dunes up to 8 meters above their surroundings (Havlíček 2004). This was possible due to lack of high standing vegetation blocking the wind and stabilizing the soil. Warming about 9 thousand years ago allowed forestation. These dunes, (locally called “hrúdy”) here referred to as hummocks were suitable for the first settlers. Settlers of the emerging Great Moravian Empire around the 8th century shaped the location further by more deforestation resulting in lower altitudinal differences throughout the area via stronger floods (Miklín et al. 2010). This change of water conditions shifted species composition towards softwood species like willows or poplars (Grulich 1992). During the late 20th century, water conditions were also seriously affected by alterations of river flow finishing with construction of The Nové Mlýny reservoirs. This caused irreversible damage to riparian ecosystems and limited floods. Locals later tried to restore the flood regime artificially starting in 1992 (Pražák et Kloupar 1996). The restoration was fairly successful but could not fully simulate historical conditions.

While hummocks are no longer as high, they are still elevated above adjacent areas providing drier climate, hence hosting a different set of species (Fillipov 2007). This forms a mosaic of varying ground water levels and it is possible to find species bound to dry and wet conditions fairly close together. Flinn et al (2008) present an opposite case with similar results, where small wetlands dispersed in otherwise drier upland forest increased overall species diversity. Hummocks host slightly higher species diversity possibly due to increased water and nutrients stress. Pollock et al (1998) reach similar results predicting that frequently or permanently flooded areas host lower diversity; however very low frequency of flooding can also harm wetland diversity. The mosaic of water availability made by the hummocks also creates transitional areas - ecotones which are known to integrate species from multiple communities hence have higher species diversity (Kark 2013).

Light reaching the herbaceous layer is equally important, whether it is illuminating deforested soil or penetrating tree canopy. Abundant light is a crucial factor for example in seedling survival under flood-induced stress (Streng 1986). Canopy cover is negatively correlated with species diversity. Clearings have very high plant diversity, but are replanted with ash or oak and will get to similar state as plantations, eventually losing the diversity. On the other hand, solitary trees function as ecotones between forest and meadows resulting in high species diversity (Einarsson et Milberg 1999) while having relatively little canopy cover compared to closed forests.

Unlike moisture conditions, light availability was not partitioned out from management type effects as canopy cover is inherently bound to the forest type, hence feasible variation explained by management would be filtered out. For similar reasons less attention was given to light conditions as its effects are mostly explained by management effect analyses.

5.2 Effects of management on species richness and composition

Wooded meadows, meadows with occasional solitary trees, form an iconic part of the study area. Apart from their aesthetic function, old oaks connect meadows and forest together. They provide some shadow in otherwise well illuminated meadows resulting in their high species diversity. Solitary trees and their immediate surrounding area are home to many woody and herbaceous species. Richness of wooded meadows is well recognized (Kull et Zobel, 1991, Einarsson et Milberg 1999). Solitary trees are also a traditional type of management and as such contain few invasive species with almost no cover taken up by such species. They contain a high amount of naturalized archaeophytes second only to clearings. Those however have little negative effect on species diversity. As such wooded meadows host a lot of native biodiversity.

The main problem wooded meadows have is that most of the oak standards are old and sooner or late will die. In addition current management does not create new opportunities for solitary trees establishment. Unless proper actions are taken, solitary trees may become a thing of the past and restoration of this particular phenomenon will take many years.

Clearings tend to have high species diversity (Wang et Nyland 1993, Gondard et al. 2001, Pykälä 2004; but see Gilliam et al. 1995) and indeed the other management type/state, rich in species diversity, is clearings. Most of the study area is managed by simple clear-cuts up to 2 ha in size (Miklín et Čížek 2013). Standards are seldom left after harvest. They are also close together and near the forest edge which leaves large plots of land disconnected from the forest ecosystem. Considering simple species count, clearings have the highest diversity in the herbaceous layer. However when comparing total richness, solitary trees are on par with clearings. This is intuitive as clearings by definition contain almost no shrubs and standards left over can have narrower canopy due to past competition. Shade provided by solitary trees helps various shade-tolerant shrubs which have enough time to grow here as wooded meadows are stable and no mere transitional state to plantations. When clearings are examined by Shannon-Wiener diversity index they are much poorer than solitary trees. Species composition of clearings is hence much less unique compared to solitary trees.

When moisture conditions are partitioned out, clearings are even more distinct from the rest suggesting that the actual disturbance and increased illumination is what drives the species composition. Value of these species rich plots is further diminished by the fact that clearings are commonly invaded by neophytes. While invasive species take up more area in coppices, clearings have much higher invasive species count. Among species closest to clearings are such invaders as *Conyza canadensis* or *Echinochloa crus-galli*. Clearings also contain most archaeophytes. While rich, clearings host very little native flora and as such have almost no conservation value.

Timber harvesting is a large scale disturbance lacking important components for proper forest reestablishment such as deadwood (Niemelä 1997). Furthermore clearings in the study area are typically replanted with ash and oak (Miklín et Čížek 2013). Planted trees and cleared deadwood will create a homogenous close canopy forest. This is detrimental to species diversity (Duguit et Ashton 2013).

Indeed this study shows that plantations are way poorer than clearings from which they originate. As the canopy closes, non-forest species vanish and diversity drops (Halpern et Spies 1995). Compared to clearings, plantations have a much lower percentage of invasive species; cover taken up by neophytes is similar though. This suggests that canopy closure wipes out many invaders that make clearings their home. Then few shade-tolerant invaders left (such as *Impatiens parviflora*) take up a similar amount of cover. Plantations also contain less archeophytes and more native flora as trees and shrubs are mostly native species, even though occasionally neophytes such as *Juglans nigra* make up the canopy as a reminder of careless forestry habits.

Timber harvesting itself is not a problem. It has been widely shown that wood can be harvested and if proper management is utilized, species diversity does not suffer as tree retention or even clear-cuts on a small scale pose little risk to understory species diversity (Malcolm et al. 1995, Halpern et al. 2005, Fisher 2011, Zenner et al 2013). Clear-cuts in the study area are done on a large scale and with alarming frequency as 50% of the forest has been logged in the past 40 years (Miklín et Čížek 2013). Such approach is not just harmful but also unsustainable.

While the relationship of plantations to clearings is quite clear, they must also be compared with more traditional managements like coppicing and forest pasture. With the advent of first agriculture 5 to 7 thousand years ago, human settlers maintained deforested areas and open canopy forests where they pastured animals and coppiced for firewood (Miklín et al. 2010). Due to increased demand for wood during the industrial revolution forest pasture was forbidden in 1754. The ban was disregarded by the peasants till 1873 when the Liechtenstein dynasty used the military to drive the local villagers from the forest which is recognized as the advent of organized forestry in the area (Nožička 1956). Coppicing was also abandoned and even aged plantations started filling up the forests. Canopies of open forests also closed from lack of their respective disturbance (grazing, coppicing). Hence what is considered coppices, coppices with standards and pasture forests in this study are forests, which were previously managed this way.

Plantations, pasture forests and coppices with standards seem to be very similar in species diversity and composition. No change occurs when we filter out moisture conditions. This is further supported by the fact that when these three management types were tested alone, the effects of management and moisture had no shared explanatory power even though moisture explains more than management itself.

The similarity must then be from the cessation of traditional management as these forests are growing older reaching a state similar to plantations. Further analysis shows us that there are significant differences. These are however hard to interpret. It is by analyzing species composition while considering residence time and invasive statuses, that we reach well interpretable results. Univariate approaches show only small differences where coppices with standards are probably the least invaded. They have the most native species cover and the least percentage of invasive species.

Multivariate analyses shed more light on the relationship these three management types have. Pasture forests and coppices with standards as representatives of past traditional management are similar in species diversity. The contemporary practice, plantations are different. These show a close affinity to neophytic invaders and are much poorer in native flora. This would suggest that even after traditional management practices are abandoned the forests are still of higher value than homogenous plantations. There is also a positive connection between lack of native flora and invasibility (Naeem et al. 2000). Improved diversity and native flora of pasture forests and coppices with standards may also be a result of their structure. Spatially heterogeneous forests have higher species diversity (Halpern et Spies 1995). After all it seems that previously traditionally managed forests are a reasonable target for proper biodiversity protection (Lassacue et al. 2012, Vild et al. 2013).

Different results are obtained when we analyze coppices (without standards). Compared to the three previously discussed management types, coppices have higher total species richness the difference is a bit smaller when we only count herbaceous/juvenile species. A multivariate analysis shows further dissimilarity. Apart from higher species richness, these differences may be explained by considering species residence time and invasive statuses. Coppices are very abundant in invasive neophytes; even more so than clearings but only a few invasive species are present. Upon closer examination of phytocoenological data, we find that *Impatiens parviflora* is the predominant invader. On its own it takes up most of the ground layer consistently.

Coppicing is a disturbance and lets more light reach the forest floor. As coppicing is done periodically this poses little problem to species diversity, in fact coppices are well known for their exceptionally rich plant composition (Gondard et al. 2001, Ito et al. 2012). However, after coppicing is abandoned the stands naturally grow into a homogenous lower-diversity state (Nagaike et al.2003). Invasions are then very probable even more so as riparian forests are very prone to them (Pysek et Prach 1994).

Tree lines are also fairly rich in plant species. Their flora is quite distinct and tree lines tend to be in water rich areas. This is probably due to them being formed adjacent to rivers. As they tend to be narrow, species richness can be explained by their ecotonal nature (Kark 2013). Their surroundings host both shade-tolerant and shade-intolerant species and the transition to non-forested area is dominated by various shrubs increasing species diversity. They are composed of few invaders and a comparatively medium amount of native plants.

6. Conclusions

Forest ecosystems are very diverse in their structure and composition. In this study I attempted to show how flora reacts to various types of management. Examining these managements from many perspectives shows tangible differences even between very similar management types. The results then can be used to create an optimal management practice for the study area.

Perhaps a more important message is how not to manage these forests. I have found very little contemporary scientific literature dealing with such harsh and ecologically unsound management such as the one practiced in the study area. Invasive species occasionally spanning across the entire forest floor are more of a symptom of ecologically problematic practices.

There are so many methods of timber harvest that are far less destructive while still economically viable (Malcolm et al. 1995, Thomas et al. 1999, Halpern et al. 2005, Fisher 2011, Zenner et al 2013). As Miklín et Čížek (2013) pointed out, the study area is a biodiversity hotspot being erased by improper care. Even now there is still a large area taken up by valuable forests worth protecting but without a change in attitude from forest managers, we might miss our chance.

Traditional management may no longer be economically feasible but still worth doing in order to protect local species diversity. Money gained from timber harvesting can be spent to reintroduce coppicing (both with and without standards) or wood pasture. Such managements are traditional in the study area and create a mosaic of forests with varying structure. Such mosaic of diverse spatial and temporal structure would positively benefit not just plants but various other taxa.

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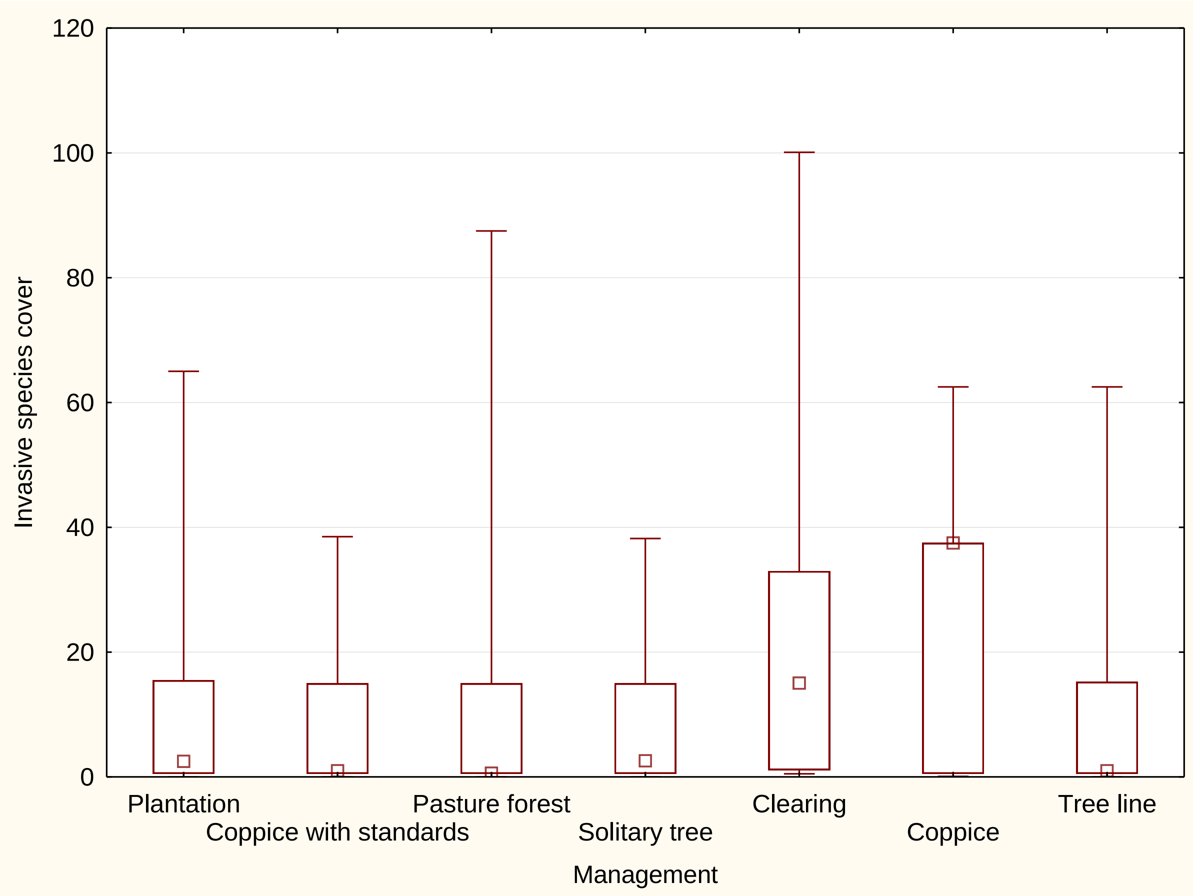
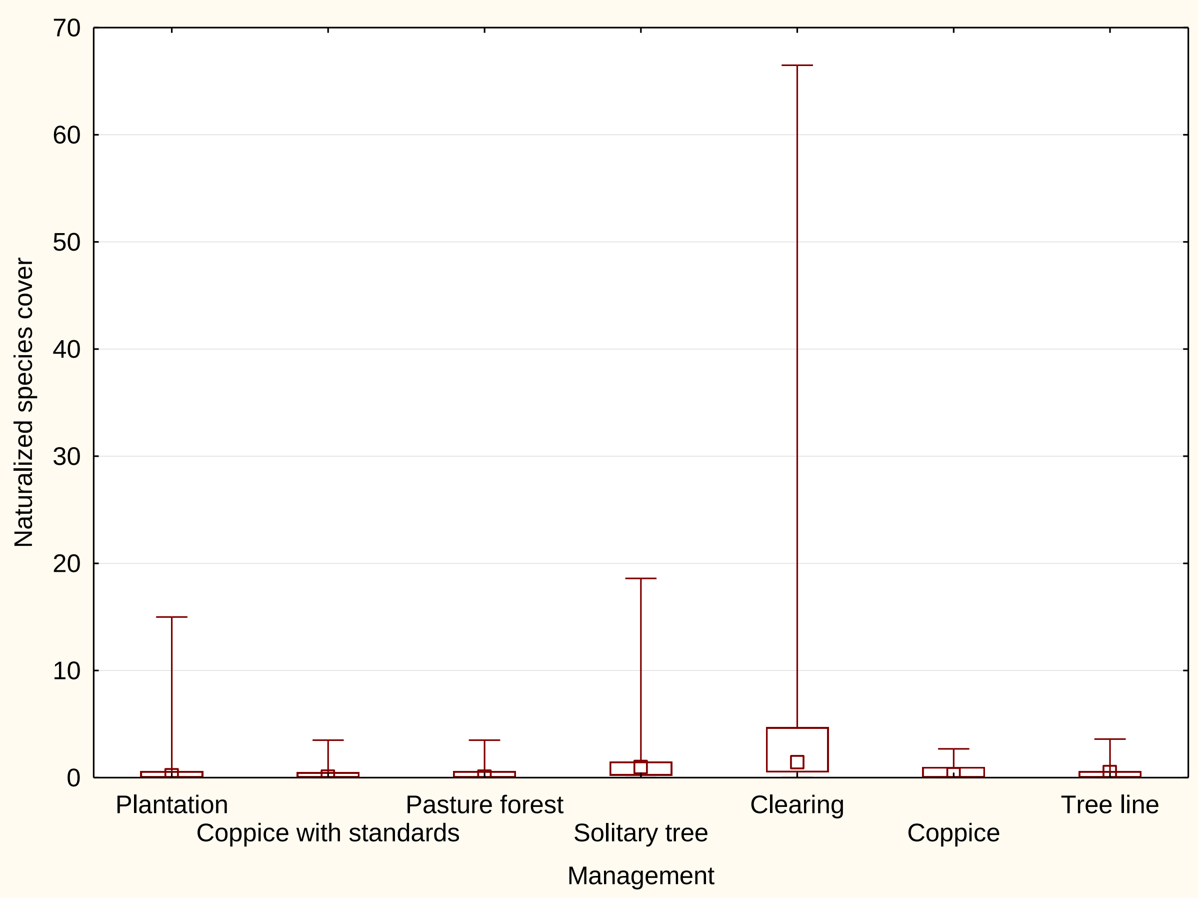
8. Supplementary material

One Way ANOVA: F=2.67; DF=6, 260; **p=0.016**



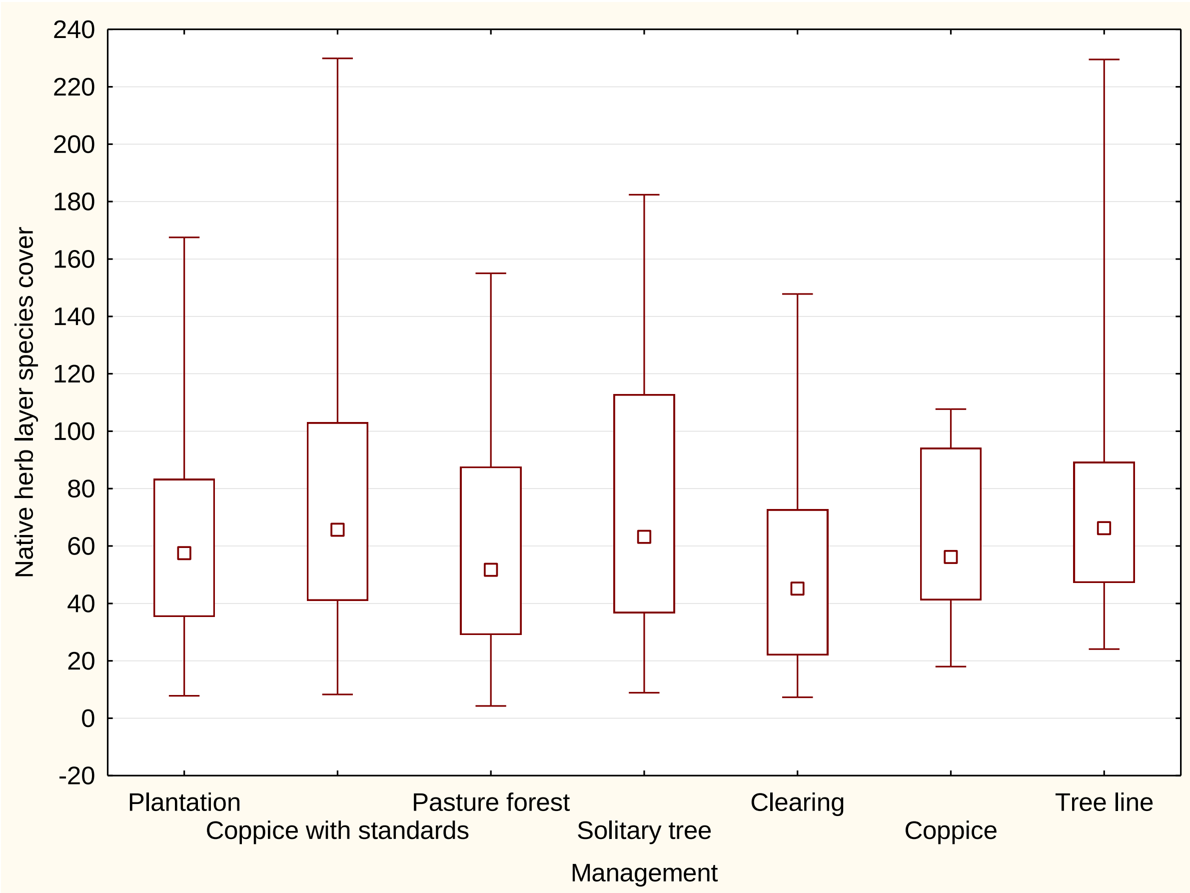
Supplementary Figure 1: Dependence of invasive species cover on management types. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

One Way ANOVA: F= 4.43; DF=6, 260; **p<0.001**



Supplementary Figure 2: Dependence of naturalized species cover on management types. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.

One Way ANOVA: F= 1.32; DF=6, 260; p=0.249



Supplementary Figure 3: Dependence of native E1 (herb/juvenile) species cover on management types. Central point denotes median, box denotes 1st and 3rd quartiles. Vertical lines denote 2.5% confidence intervals.