CARBON SEQUESTRATION OF FLOODPLAIN FORESTS: A CASE STUDY FROM HUNGARY, MAROS RIVER VALLEY

V. Cseh, M. Kiss and E. Tanács

Abstract. Model-based assessment of the carbon storage potential of different types of forests is an important task in the context of climate change and green infrastructure development goals. In our paper, we present the results of the calculations aimed at comparing carbon sequestration processes of floodplain forests with different ages and management intensities in the active floodplain of the Maros river (South East Hungary). These types of assessments can help in resolving the complex environmental management issues of these areas, characterized mainly by the conflicting interests of the forestry, water management and nature conservation sectors. The work was carried out using the CO2Fix3.2 model, based on the field database of a forest reserve and the forest inventory of the area. The main forest types are native and non-native willow-poplar stands, managed and non-managed hardwood forests (with pedunculate oak and elm species) and stands of invasive species. The results highlight the importance of managed forests with long rotation cycle and old-growth unmanaged forests from the point of view of carbon sequestration. They also draw attention to the necessity of incorporating these ecosystem services in the planning processes for a better environmental decision-making.

Key words: carbon stock modelling, CO2Fix, management intensity, willow-poplar forests, floodplain forests, Maros valley

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Introduction

Global climate change is of great importance among environmental issues. By now most scientists agree that greenhouse gases are among the key factors contributing to unfavourable changes in the planet's climate system (IPCC 1990, 2007). Carbon dioxide is one of the most important anthropogenic greenhouse gases and its atmospheric concentrations have increased since the 19th century, therefore the examination and understanding of the carbon cycle are becoming increasingly important. Vegetation plays a significant role in the global carbon cycle. Since plants extract carbon from the atmosphere during their photosynthesis, forests help stabilize the climate and mitigate the negative effects of climate change. The flow of carbon in the biosphere is part of a complex biogeochemical cycle. In order to set up the exact carbon-balance equation a better understanding is needed about each of the cycle's carbon binding or storing processes.

Due to the imminent dangers of global climate change, climate regulation through carbon sequestration is currently one of the most widely acknowledged ecosystem services of forests. The sequestered carbon shows up in the biomass increment and is stored in various stocks (e.g. stems, branches, foliage, roots and soil) until it returns to the atmosphere as a result of turnover or logging. Earlier it was generally thought that ageing forests should be considered carbon-neutral (Odum 1969). This was based (among others) on the assumption that the growth trends of individual trees and even-aged monospecific stands can be directly extended to natural forests. However, it was found later that growth and carbon acquisition in old natural forests cannot be extrapolated from the productivity of even-aged stands (Carey *et al*. 2001).

Recently research on the effects of forest management intensity has shown that forest management and disturbances affect forest soils and biomass carbon stocks and emissions to the atmosphere (Luyssaert *et al*. 2011). Harvesting frequency and structural retention significantly affect mean carbon storage, and mean carbon sequestration is significantly greater for non-managed stands compared to any of the active management scenarios (Nunery and Keeton 2010). Of the harvest treatments, those favouring high levels of structural retention and decreased harvesting frequency store the greatest amounts of carbon (Neilson *et al*. 2006, Taylor *et al*. 2008, Nunery and Keeton 2010). Greater harvest intensity results in less carbon storage, and the carbon in wood products does not make up for harvest losses (Nunery and Keeton 2010, Fischer 2013).

Hungarian forests are considered important carbon sinks (Somogyi 2008); in fact, they are the only significant sinks in the greenhouse gas balance of Hungary (Kis-Kovács *et al*. 2011). Although there are some studies regarding their carbon sequestration capacities (e.g. Führer and Molnár 2003, Balázs *et al*. 2008, Juhász *et al*. 2008, Kiss *et al*. 2011), the floodplain forests of Hungary have not yet been specifically studied from this respect.

Since the river regulations of the 19th century, the floodplain forests of Hungary have been constrained between the river and the flood control dams. Their development is defined by the hydrological and geomorphological environment. These controls affect the vegetation at the patch scale through soil quality (hydrology and fertility), stability of substrate and floodplain hydrology/ hydrogeology (Brown *et al*. 1997). In their natural state, floodplains are notable for their diverse habitats and vegetation. Geomorphological complexity is the key for this diversity (Harper *et al*., 1995), but both the complexity and attendant biodiversity are only present if there is no intensive land use on the floodplain.

There are a number of unresolved problems related to floodplain forests in Hungary (Czeglédi 2004). Beside the local inhabitants, their fate is defined by three main stakeholders, acting under different regulations: nature conservation authorities, private and state forest managers, and water managers (with a high priority on flood prevention). The different priorities of these actors mean that their interests are often in conflict.

The total area of the once widespread floodplain willow-poplar woodlands in Hungary is currently approx. 21000 ha (Bölöni *et al*. 2008). Much of the stands were historically converted into meadows, farmlands or orchards, later their sites were occupied by American poplar plantations, with an uncharacteristic, weed-infected herb layer (Bartha 2001). Their high proportion is primarily due to economic reasons, because establishing such non-native plantations was more profitable, and the existing support systems were of no use in preventing this process (Dobrosi and Szabó 2001). The current legislation supports the plantation of native species wherever possible (XXXVII/2009), however, as a result of the former river regulations, the water regime is changing and that poses a considerable threat to the regeneration of the native species, which induces a further increase of the plantation area. Another serious problem is the presence of invasive plants, which slow down or prevent the regeneration of the native species. In some stands the younger generations of trees consist almost entirely of *Acer negundo* and *Fraxinus pennsylvanica* (Bölöni *et al*. 2011). Although naturalness of the species composition of the floodplain willow-poplar forests tends to be low (due to the presence of the invasive species), these forests still have considerable merits from the nature conservation point of view: due to the rapid growth and short life span of the willow and poplar species, a near-natural stand structure can form in a relatively short period of time (Bartha and Gálhidy 2007). This in turn may lead to the appearance of protected animal species.

The ecosystem services approach provides a well applicable framework for resolving the above-mentioned conflicting interests. Therefore, it is important to see how different management scenarios affect the different services. In this research we examined how different treatments affect the carbon-sequestration potential of the forests of the lower Maros valley and what would be the optimal mode of management from this point of view.

Material and methods

1. Study area

Investigations were carried out on the floodplain of the Maros river near Szeged, Hungary (Fig. 1). Most of the forests in this area are plantations of both native and non-native species. There are also a forest reserve and some stands of willow-poplar forests. The main tree species include: pedunculate oak (*Quercus robur*), white poplar (*Populus alba*), black poplar (*P. nigra*), hybrid poplar (*P. × euramericana*), the Hungarian subspecies of narrow-leafed ash (*Fraxinus angustifolia* ssp. *pannonica*), European

ash (*F. excelsior*) and American ash (*F. pennsylvanica*), white willow (*Salix alba*) and European white elm (*Ulmus laevis*). In addition, black walnut (*Juglans nigra*), white mulberry (*Morus alba*), and sporadically hybrid plane (*Platanus × hybrida*) and common hackberry (*Celtis occidentalis*) also occur.

Eleven sample areas were selected along the Maros river from Makó to Szeged. These areas can be characterized by different species composition, age classes and management intensity (Table 1, Fig. 1).

Table 1. Management intensity and naturalness of the different forest types in our study area. Notations: 1: most natural stands with little or no management; 2: managed mixed and native stands; 3: native monocultures or non-native forests. Abbreviations: An: *Acer negundo*, Fp: *Fraxinus pennsylvanica*, Pa: *Populus alba*, Pn: *Polulus nigra*, Ul: *Ulmus laevis*, Qr: *Quecus robur*.

| Age (year)	Management intensity and naturalness		
	1	2	3
0-20		A Poplar stand with native species (Pa, Pn)	B (1,2) *Populus × euramericana* plantation stands
20-50	C Willow-poplar forest at the site of an oxbow lake	D Native poplar stand mixed with American ash (Pa, Fp)	E Oak stand mixed with American ash (Qr, Fp)
50-	F (1,2,3) Forest reserve: willow-, poplar-, European white elm-dominated stands	G Riverbank protection forest (Pa, Ul, An)	H Oak stand (Qr)

Fig. 1. Study areas along the Maros river. Notations: 1: most natural stands with little or no management; 2: managed mixed and native stands; 3: native monocultures or non-native forests.

Most of the study area on the right bank of the river is under protection and belongs to the Körös-Maros National Park. There is a strictly protected forest reserve near the mouth of the river as well. All human activity is prohibited in the core area of the forest reserve, therefore it is completely unmanaged. The stands here are 60 year-old willow-poplar forests with a slight shift towards oak-elm-ash forests, showing a diverse structure and a relatively high species diversity. The buffer zone is considered strictly protected which in theory makes it possible for forest managers to intervene. The stands in the reserve are infested with invasive species, especially American ash, which composes most of the regeneration layer. Less intensively managed stands outside the reserve include Natura2000 areas and other protected areas where management is allowed only with limitations. These stands also mainly consist of native species. Finally there are the intensively managed plantation forests, mainly of *Populus × euramericana*. One of the sample stands is situated outside the protected area, near the mouth of the river at the town of Szeged.

2. Field surveys

Each sample corresponds to a forest section, except in the reserve, which is rather diverse, and therefore it cannot be characterized properly by the usual unit of the forest inventory. The species composition and the age classes of the other stands were characterized by the data of the forest inventory. However, in different stands of the reserve, a forest structure survey was conducted in circle plots with 20 m radius, in which the position, diameter at breast height, crown class and species of each tree were recorded. The data of 3 plots in 3 different types of stands were chosen. F1 is a hollow with a few large old willow trees and lots of young American ash trees on the higher banks of the hollow. F2 is dominated by older poplar trees (both black and white) and European white elm in the second layer, and lots of smaller American ash trees. F3 is situated on slightly higher ground, which is dominated by European white elm. *Acer negundo*, together with a few older willows and lots of young American ash trees also occur in this stand.

Due to regular flooding, the soil properties of the floodplain can be considered fairly homogeneous. Soil samples were taken from a recently planted stand in order to measure the initial carbon content of the soil and to estimate the proportion of raw and recalcitrant humus forms. Measurements of the soil properties (humus content, proportion of raw and recalcitrant humus forms) were carried out according to the MSZ21470/52-83 standard.
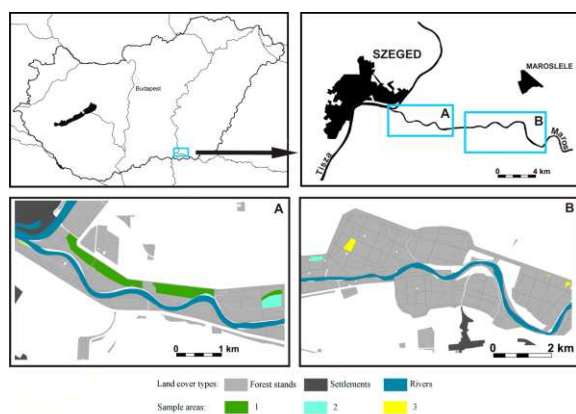
3. Brief description of the CO2Fix model

The CO2Fix model was chosen for the analysis. CO2Fix (v. 3.2) is a simulation model developed as part of the CASFOR II project. It quantifies the carbon stocks and fluxes in the forest biomass, the soil organic matter and the wood products chain (Masera *et al.* 2003; Schelhaas *et al.* 2004). These are estimated with a time-step of one year using the 'cohort' as a unit, where each cohort is defined as a group of individual trees or species, which are assumed to exhibit similar growth. The model consists of six modules: biomass, soil, wood products, bioenergy, financial, and carbon accounting.

The biomass module converts volumetric net annual increment data to the annual carbon stock of the biomass compartment. Turnover and harvest parameters drive the fluxes from the biomass to the soil and the products module, respectively.

The model has a soil module known as Yasso (Liski *et al.* 2005) which simulates the dynamics of carbon in the soil, taking into account the decomposition of the organic matter, long term storage of carbon and its flux back to the atmosphere. Soil module inputs include litter from turnover and mortality processes and logging slash forms and the initial litter quality and the effect of climate on decomposition are also taken into account.

The fate of the harvested timber is followed via the products module. Through the decomposition of waste, this is also related to the atmosphere.

The carbon content of firewood and (after a while) of the wood products get back to the atmosphere (the latter through waste incineration); this is calculated by the bioenergy module.

The carbon accounting module follows the changes of the carbon content of the atmosphere and determines the accounting units gained in a prospective related climate policy project.

Finally, the financial module calculates the revenue based on the expenses and incomes from the management.

The total carbon content of the system is obtained by adding up the amount of live biomass and soil carbon content and the carbon stored in wood products. The overall effect on the climate system depends on the changes of the carbon content and the so-called avoided emission. Avoided emission characterizes how much less carbon dioxide is released into the atmosphere through substituting fossil fuels with biomass; it is also calculated by the bioenergy module. In this analysis the financial and the bioenergy modules were not used.

4. Model parameterization

Current annual increment and other yield data were taken from yield tables (Table 2). We have not found yield tables for all species, especially those that are economically less important in Hungary. Therefore data of relative or similar species were used, based on information from the literature (Veperdi 2008).

Table 2. Yield tables used in the present study.

Species	Reference
Ash (*Fraxinus excelsior*)	Kovács (1986)
Hybrid poplar (*Populus × euramericana*)	Halupa and Kiss (1978)
Pedunculate oak (*Quercus robur*)	Kiss *et al.* (1986)
Sessile oak (*Quercus petraea*)	Béky (1981)
White poplar, grey poplar (*Populus alba, Populus × canescens*)	Rédei (1992)
White willow (*Salix alba*)	Palotás (1969)

The wood density data were taken from Somogyi (2008), and in the case of hybrid poplar from Molnár and Komán (2006). For the calculation of the carbon content of wood, the IPCC default (0.5 t C/t biomass) was used. The relative growth of the branches was calculated based on branch proportion tables (Sopp and Kolozs 2000), where the values were assigned to age groups according to the tree size. Density-dependent mortality was estimated only for the non-managed stands based on the yield tables, while management mortality was defined according to expert opinion (from the state forest manager). Approximate thinning-harvest data were also provided by the local state forestry company.

The mean temperature and precipitation data were gathered from the National Meteorological Service [1], while the growing season was defined as the period from March till October. In the products module the second default dataset (low processing and recycling efficiency) was used, slightly modified on the basis of information from the state forestry company.

We have run the simulation for a period of 120 years, according to the longest rotation cycle used in the area (for oak stands). Each species were modelled separately and the results were added up for each stand after being weighted according to the species' proportion at the specific sample site. In the case of the most natural stands, we added some cohorts with time, thus simulating successional development and species changes. The time of the addition and the species of the new cohorts were based on forest inventory data and the field survey data.

Results and discussion

The results of the simulations are presented in Table 3 and Fig. 2 while Figs 3-7 and Appendix Figs 1-6 show how the carbon content changes with time in the different compartments and overall in the sample areas.

Table 3. The maximum carbon content values in the sample areas [tC/ha]. Stands highlighted with grey are not harvested.

Age (year)	Management intensity and naturalness		
	1	2	3
0-20		A: 65.11	B1: 116.13 B2: 95.04
20-50	C: 167.33	D: 105.31	E: 283.87
50-	F1: 196.31 F2: 217.55 F3: 173.39	G: 122.53	H: 236.90
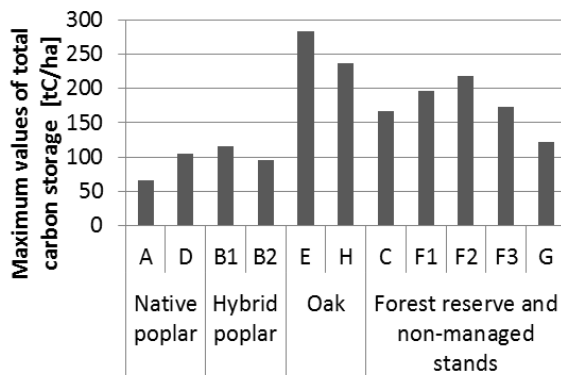
Fig. 2. The maximum carbon content values in the sample areas [tC/ha].
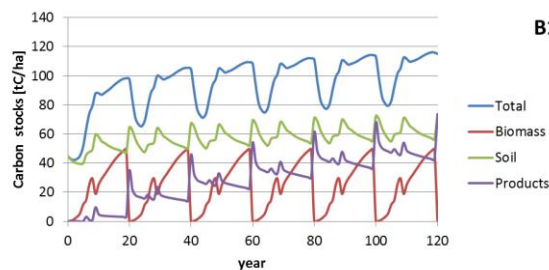
Fig. 3. Carbon stocks in the main compartments of the sample area B1 (hybrid poplar plantation stand).
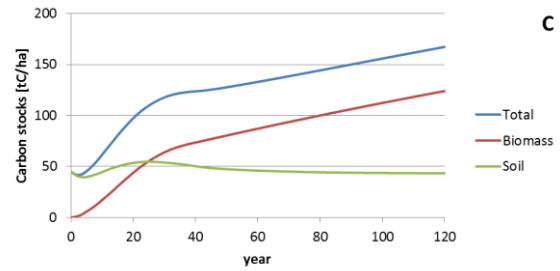
Fig. 4. Carbon stocks in the main compartments of the sample area C (willow-poplar forest at the site of an oxbow lake).
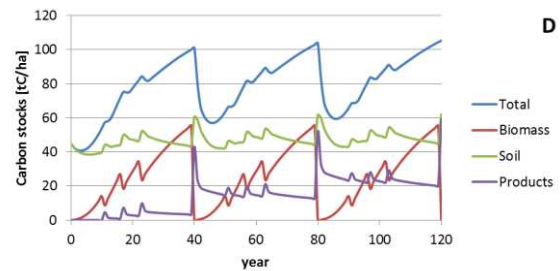
Fig. 5. Carbon stocks in the main compartments of the sample area D (native poplar stand mixed with American ash).
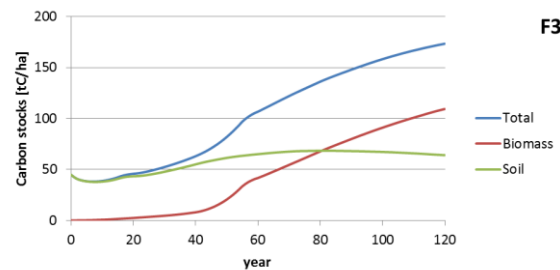
Fig. 6. Carbon stocks in the main compartments of the sample area F3 (forest reserve, European white elm dominated stand).
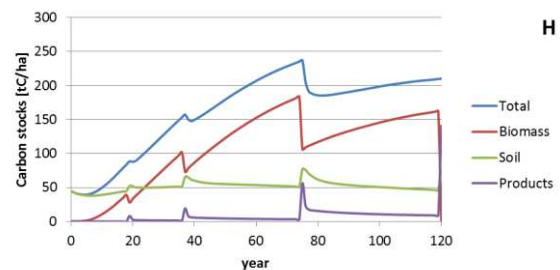
Fig. 7. Carbon stocks in the main compartments of the sample area H (oak stand).

Among the managed forests, the oak stands can be characterized by he highest carbon storage potential. Beside the species characteristics and the longer rotation cycle, the reason for this is mainly the high proportion of long-lasting products (e.g. furniture) made of oak wood.

The carbon storage potential of the hybrid poplar stands is much lower than that of the oak stands. The carbon stocks in the different compartments of the hybrid poplar stands basically reflect the management regime, since they are generally characterized by rapid growth (depending on the variety) and consequently a very short rotation cycle. It should be noted that the continuous growth of the total carbon content in the modelled results is somewhat doubtful. The modelling process in this case should be further refined by introducing soil carbon loss resulting from the soil preparation works when planting the new stands (see Somogyi *et al.* 2013) as well as a more precise parameterization of the lifecycle of the derived wood products. The continuous increase in the amount of carbon stored in the products is due to the fact that some of them are supposed to end up in landfills where decomposition is very slow. Even though this proportion has been assigned a small value (around 5%) in the model, in the case of short rotation cycle (when lots of products are produced), the carbon storage of the products added up.

According to the model, the carbon storage potential of the native poplar stands was similar, but slightly lower than in the case of the hybrid poplars. However, it should be taken into consideration, that the carbon storage potential of native poplar stands may be higher in reality: due to partial restrictions from the protected status, clear-cutting and the subsequent complete soil preparation are not allowed in these stands. Therefore, emission from the soil is probably less than in the case of non-protected stands.

In the stands of the forest reserve and the other non-managed stands, a continuously increase of the carbon storage can be clearly seen. In the case of the poplar forests, it exceeds the values of the managed poplar stands. However, the results should be further refined by introducing an increased mortality at higher ages, which were not included due to a lack of dynamics-related data.

In conclusion, the older floodplain forests can be considered significant carbon sinks. In the case of the poplar species, less intensive treatment and longer rotation cycles are more favourable from the carbon sequestration point of view, mainly due to less soil disturbance, and the generally short life cycle of the products coming from the plantations (mainly paper and packaging materials), which thus retain carbon only for a short time.

Although the low number of samples does not allow carrying out statistical comparison, the results of the simulation at the current age of the stands were compared to calculations based on the actual forest inventory data. As Table 4 shows, the results seem to be realistic, although the modelled results are generally higher, especially in the case of the oak forests. The reason for this remains to be investigated; a knowledge of the site history would be necessary (locally, the management regime can be altered or the specific stand could have been affected by factors unaccounted for – e.g. biotic or abiotic damage).

Table 4. Comparison of the carbon storage of the biomass compartment [tC/ha] based on the model results and the forest inventory

Sample areas	Age (year)	Carbon storage of the biomass [tC/ha]	
		Forest inventory	Modelled
B1	10	22.80	25.11
B2	20	37.13	39.34
D	21	37.68	31.49
E	58	117.20	177.73
H	91	110.58	134.31

Issues to be fixed and further research

Several problems occurred in the course of the analysis and especially the model parameterization. As most existing carbon sequestration models, CO2Fix can be best used to describe the processes of managed forests with few tree species. A serious drawback of the model is that the proportions of the cohorts cannot be defined, and the input data in the products module cannot be given for each cohort separately. We fixed this by creating a separate file for each species. However this makes the modelling of between-cohort interactions, e.g. competition, impossible. The final results were then weighted according to the proportion of the species in the stand. Another issue probably affecting the final results is that the soil carbon loss following clear-cutting and replanting cannot be directly included in the model.

Due to lack of data the natural dynamics of the floodplain forests could only be characterized in a limited manner and some further important additions would be required in the interest of getting more realistic results. One such addition is density-independent mortality, which in the case of floodplain forests is mainly caused by higher-than usual, longer-lasting or icy floods (or possibly biotic effects). A more precise parameterization of mortality as a function of age and regeneration dynamics should also be included. A very important aspect would be the carbon content of the shrub layer, which is currently not possible to include. In general, there is a lack of data for those tree and shrub species which are not considered economically

important. The most important differences between a managed and a natural forest lie in the diversity and dynamics of the latter, therefore, simplification based on data from managed stands tends to favour such stands when a comparison is made. In the future, we plan to concentrate on refining the model, which requires further research concerning these issues.

Acknowledgment

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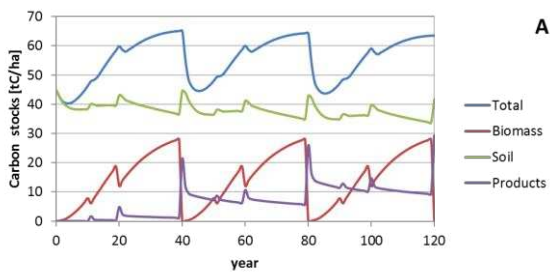
Appendix

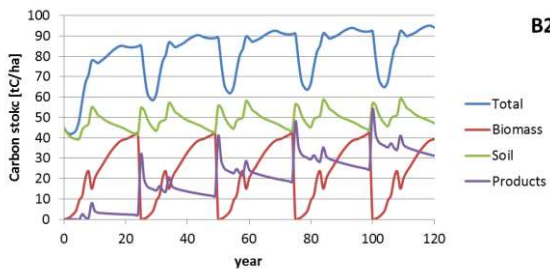Fig. 1. Carbon stocks in the main compartments of the sample area A (poplar stand with native species).

Fig. 2. Carbon stocks in the main compartments of the sample area B2 (hybrid poplar plantation stand).
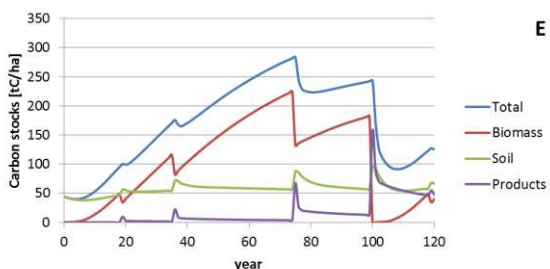

Fig. 3. Carbon stocks in the main compartments of the sample area E (oak stand mixed with American ash).
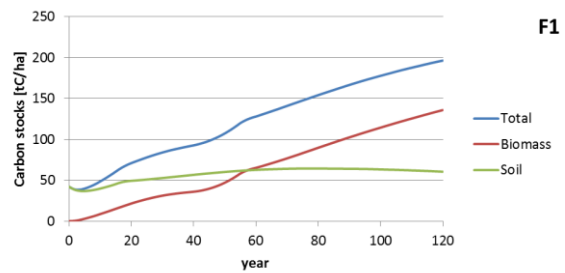

Fig. 4. Carbon stocks in the main compartments of the sample area F1 (forest reserve, willow dominated stand).
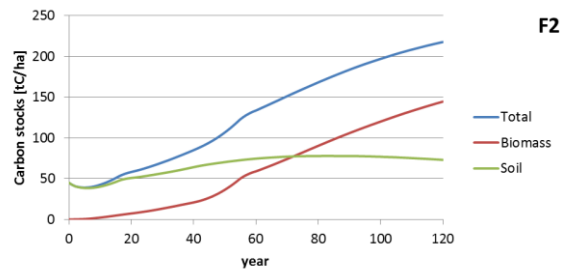

Fig. 5. Carbon stocks in the main compartments of the sample area F2 (forest reserve, poplar dominated stand).
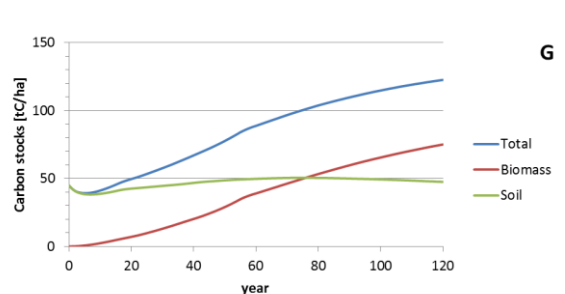

Fig. 6. Carbon stocks in the main compartments of the sample area G (riverbank protection forest).

POST-FIRE REGENERATION OF A FOREST-STEPPE: VEGETATION STATUS 20 YEARS AFTER THE FIRE EVENT

L. Erdős

Abstract. Fires played an important role in the natural dynamics of the forest-steppes, but human activity has modified the regeneration capacity of the vegetation: for example, post-fire immigration of the native species is less efficient, due to habitat fragmentation. On the other hand, alien species (including invasives) are positively affected by fires. During the past few decades, several human-induced fires happened in the sandy forest-steppes of the Danube-Tisza Interfluve. Unfortunately, little is known about the regeneration processes. My aim was to compare two neighbouring forest-steppe segments, one of which burned down in 1996, the other remained intact. I prepared coenological relevés in both segments, and compared them, based on PCoA-ordination, differential species, species number, social behaviour types, species' coenological preferences and species' light requirement. The ordination and the social behaviour type spectra suggested that, almost two decades after the fire event, differences are not very pronounced any more. However, there were more light-demanding species in the burned section. The explanation for this may be that the canopy layer became more open due to the fire. The fire increased the species number of the forest patches, but this was partly due to the alien species. It can be concluded that, although fires had an important role in the natural dynamics of forest-steppes, and the regeneration may be fast, fires are hazardous at persent. If invasives occur in the region, there is a high risk that they become more abundant.

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Introduction

In the northern temperate zone of Eurasia, there is a transitional belt, the forest-steppe zone between the closed forests and the grasslands (Walter and Breckle 2002). This zone reaches its western limits in the Carpathian Basin (Kovács-Láng et al. 2000). The forest-steppes of the Carpathian Basin are charaterized by small forest patches separated by grasslands (Wendelberger 1989). In several mixed woody-herbaceous ecosystems worldwide, wildfires play an important role in the vegetation dynamics (e.g. Burkhardt et al. 1976, Archer et al. 1988, Vera 2000, Roques et al. 2001). Similarly, there is strong evidence that fires were part of the natural dynamical processes in the forest-steppes of the Carpathian Basin (Magyari et al. 2010). However, little is known about the frequency and intesity of the fire events. Moreover, it is largely unknown how human activity modified the pattern and the effect of fires. For example, fires are often suppressed in natural areas. However, if they do occur, regeneration is modified due to several factors. For example, natural and semi-natural areas are limited in size, and they are isolated, hindering the re-establishment of several plants. On the other hand, invasive species are often positively affected by fires (Máté 2014). It has been observed that the major woody species react differently to fires, possessing different resistance and resilience properties (Molnár 2009). Unfortunately, there is a lack of detailed studies concerning the effects of fires on vegetation

properties and recovery processes, except for a few sporadic observations (e.g. Molnár 2009, Bölöni et al. 2011, Erdős et al. 2013). Detailed analyses have been carried out on the post-fire regeneration of extrazonal forest-steppes on dolomite bedrock (e.g. Tamás and Csontos 1998).

During the past few decades, some human-induced fires occurred in Hungarian forest-steppes (e.g. Bölöni et al. 2011, Erdős et al. 2013). From a nature conservation point of view, it would be desirable to gain a better understanding on their regeneration processes, so that it could be decided what kind of conservation measures are necessary to support regeneration and prevent the loss of natural values.

In this study, my aim was to observe post-fire vegetation development in a protected forest-steppe area. I compared a forest-steppe segment that burned twenty years ago with an intact segment. I wanted to find out whether the burned segment proceeds towards the original state, or a modified direction emerges, e.g. due to invasive species. My goal was also to evaluate how vegetation structure and composition differs between the two sections. I hope that my results will support efficient conservation measures.

Material and methods

The study was carried out in the protected forest-steppe area near the village Ásotthalom (south-eastern part of the Danube-Tisza Interfluve, Hungary, N 46°12', E 19°47'). The climate of this region is semiarid with mean annual temperature of 10.6°C (Ambrózy and Kozma 1990) and mean annual precipitation of 572 mm (Fröhlich in Gaskó 2009). In the study area, there are small sand dunes. Soils are humus-poor sandy soils, except for the forest stands, which have soils of slightly higher humus content and a buried layer of brown forest soil (Bodrogközy 1982). The vegetation is built up by forest patches (*Populo canescenti-Quercetum roboris, Populus alba* variant), fescue steppes (*Festucetum vaginatae*), annual sandy grasslands (*Secali sylvestris-Brometum tectorum*) and dwarf shrubs (*Molinio-Salicetum rosmarinifoliae*) (Bodrog-közy 1957). The northern section of the study area burned down in 1996 (Gaskó 2009), while the southern part remained intact. Since the northern section was dominated by large forest patches, with only very small grasslands, the comparison of the burned and intact sites was possible only for the forest patches. Canopy cover varies between 40-60%, dominated by up to 15-16 m tall silver poplar trees (*Populus alba*). In the shrub layer, *Crataegus*

monogyna is the single typical species, although *Berberis vulgaris, Ligustrum vulgare* and *Rhamnus cathartica* are also frequent. The herb layer is generally sparse, but its cover increases considerably in the openings and on the edges.

For the study, 20 plots were established in the nature reserve, 20 m × 20 m each. Ten plots were randomly located in the burned area, and ten plots in the intact segment. Coenological relevés were made in May 2014. Percentage cover of all vascular plant species was estimated visually.

A PCoA analysis was carried out on presence-absence data using the program package SYN-TAX 2000 (Podani 2001). Comparison of the plots was made with the Yule coefficient.

Differential species between the two groups (burned vs. intact) were identified with the software JUICE 7.0 (Tichý 2002), by computing phi-values as indicators of species concentration in one of the relevé groups (Tichý and Chytrý 2006). Nonsignificant diagnostic species were excluded with Fisher's exact test.

For each relevé, total species number, the number of native species as well as the number of non-native species were calculated, and values were compared between the burned and intact sites, using Mann-Whitney U-test. Data were visualized with box-plots. For this analysis, I used the program Past 2.15 (Hammer et al. 2001).

The spectra of the social behaviour types and of the species' coenological preferences were used to compare the state of the burned area with the intact one; categorization was based on the work of Borhidi (1995). To assess the light conditions of the relevés, the spectra of the relative ecological indicator values for light demand were calculated, applying the indicator values of Borhidi (1995). In all cases, calculations were based on the frequency of the species.

Results

In the 20 relevés, a total of 113 plant taxa were identified. In the ordination scattergram, the groups of the intact and the burned relevés showed a moderate overlap (Fig. 1).

I found the following 14 significant differential species: *Silene otites* (p<0.001); *Acer negundo, Dianthus giganteiformis* ssp. *pontederae, Thymus pannonicus* (p<0.01); *Dactylis glomerata* agg., *Medicago minima, Pimpinella saxifraga, Ranunculus polyanthemos, Silene latifolia* ssp. *alba, Solidago virga-aurea, Thesium linophyllon, Verbascum lychnitis, Vicia angustifolia, Vicia hirsuta* (p<0.05). All of them were diagnostic for the burned section,
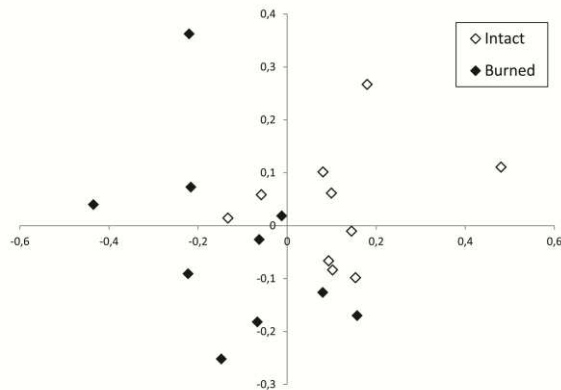
Fig. 1. Ordination scattergram of the 20 coenological relevés. Percentage variances explained by the first two axes were 30.71% and 16.65%, respectively.

while the intact section did not have any diagnostic species.

Species number was significantly (U=3.5, p<0.001) higher in the burned relevés than in the intact ones (Fig. 2a). The difference was also significant if only the native species were considered (U=5, p<0.001) (Fig. 2b). The number of non-native species was also slightly higher in the burned relevés, but the difference was not significant (U=33, p<0.196) (Fig. 2c).

Regarding the social behaviour types, no great differences could be seen between the burned and the intact sections (Fig. 3): it could not be concluded that species indicating disturbance were more frequent in either of the two groups.

If the light indicator values were considered, differences were not great, but the trend was obvious (Fig. 4). Species preferring shaded areas (categories L3 and L4) were more frequent in the intact section. In contrast, plants with a higher light requirement (categories L7, L8 and L9) were more frequent in the burned section, although the difference was minor in the case of category L7.

Species' coenological preferences differed considerably among the two groups. The greatest differences were found regarding species of natural and semi-natural grasslands and those of forests, the first group being more typical in the burned relevés, the second group in the intact ones (Fig. 5).

Discussion

Fires played an important role in the natural dynamics of the forest-steppes of the Carpathian Basin (Magyari et al. 2010). During the last few decades, several human-made wildfires have occurred in the forest-steppes of the Danube-Tisza
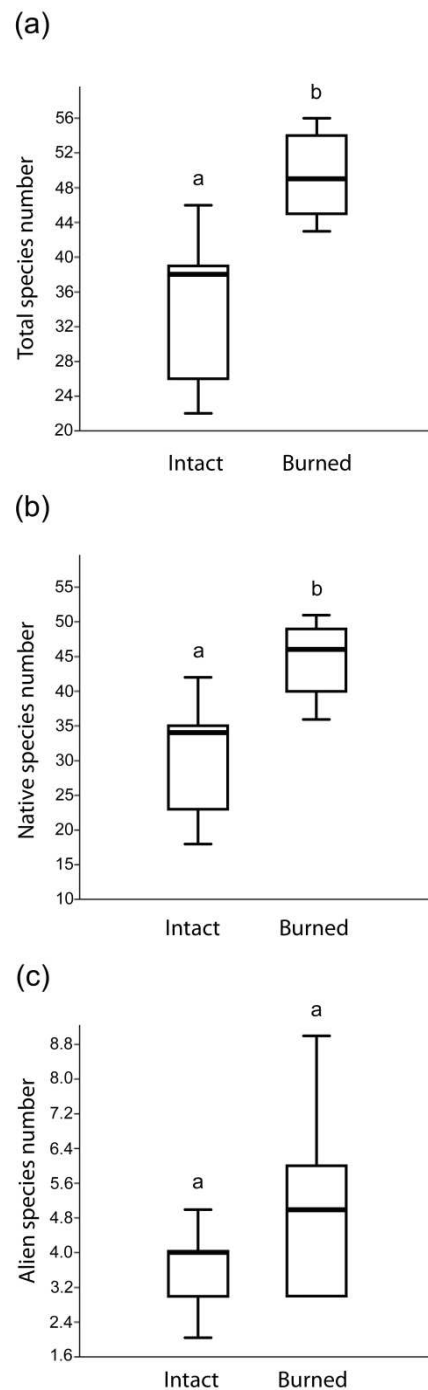

Fig. 2. Species number of the intact and the burned forest-steppes. (a) all species, (b) native species, (c) non-native species.

Interfluve (Bölöni et al. 2011), yet little is known about their effect and about the post-fire regeneration of the vegetation. The aim of this study was to contribute to the understanding of the role of fires, by comparing a burned and a neighbouring intact forest-steppe segment, almost 20 years after the fire.
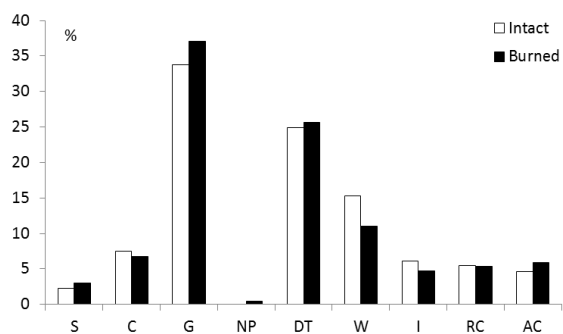

Fig. 3. Spectra of the social behaviour types in the intact and the burned sections. S: specialists, C: competitors, G: generalists, NP: natural pioneers, DT: disturbance-tolerants, W: weeds, I: introduced species, RC: ruderal competitors, AC: aggressive alien competitors (invasives).
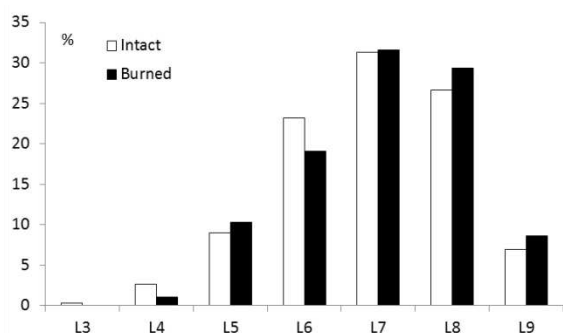

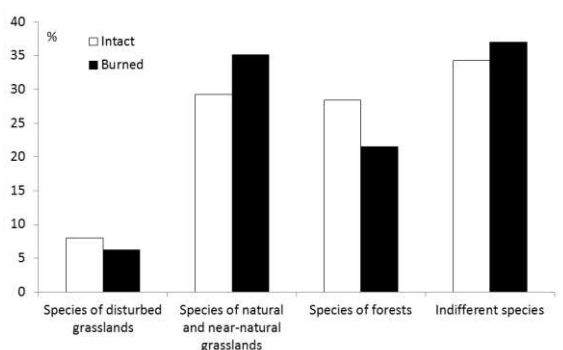Fig. 4. Spectra of the relative indicator values for light in the intact and the burned sections.

Fig. 5. Spectra of the species' coenological preferences in the intact and the burned sections.

The burned and the intact forest-steppe sections were moderately different, with a slight overlap in the ordination space (Fig. 1). Also, social behaviour type spectra did not show marked differences (Fig. 3). This probably indicates that twenty years of regeneration was not enough to reach the pre-fire conditions, but differences are not very pronounced any more. Although conclusions must be drawn with caution when using space for time substitution, it seems likely that regeneration proceeds towards the original (i.e. pre-fire) state, and not on an entirely different pathway. It has been observed that regeneration processes after the fire event may be relatively rapid, especially for the *Populus* individuals, although *Juniperus communis* regenerates slowly (Bölöni et al. 2011). The results of the present study reinforce these earlier observations. Moreover, since *Juniperus communis* does not occur in the study area, its slow regeneration does not hinder the regeneration processes of the habitat.

The differential species of the burned section were mostly plants with a high light demand (e.g. *Dianthus giganteiformis* ssp. *pontederae*, *Medicago minima, Silene otites*), typical of open grasslands. The spectra of the indicator values for light demand showed a similar pattern: plants preferring shaded areas were more frequent in the intact section, while light-demanding plants were more typical in the burned relevés (Fig. 4). Similar conclusions could be drawn from the coenological preference spectra: forest-related species were more frequent in the intact relevés, and grassland-related plants were more typical in the burned section (Fig. 5). It seems that the canopy became more open due to the fire, favouring the establishment of plants of grasslands. Although *Populus alba* grows very quickly, two decades were obviously not enough for the canopy layer to close. As more and more trees reach the canopy, the light-demanding species will probably be adversely affected, although some of them may survive in the forest patches for a long period.

I found that the fire event increased the species number of the forest patches (Fig. 2). This supports the idea that fires may have been important natural disturbance events in the forest-steppes, increasing the diversity of the forest patches. However, my study has shown that the higher species number in the burned segment was partly due to the alien species. At present a high number of alien species can be found in the regional species-pool. Some of them have a competitive advantage after the fire. This has been well-known for *Robinia pseudo-acacia* (Bartha et al. 2006), but the present study has revealed that it is true for other non-native species as

well. Thus, although fires had an important role in the natural dynamics of forest-steppes, they are hazardous at present. Although post-fire regeneration may be relatively fast, the alien plants pose a considerable threat to the integrity of the forest-steppes. This is especially true for areas where alien species have higher cover values than in the study area; in those cases, they may out-compete native species (personal observation).

Given the present conditions, wildfires in the forest-steppes should be prevented in the Carpathian Basin. If they do occur, chance for the vegetation to regenerate relatively quickly becomes high when no invasive species are present. If, however invasives are present (which is the case for most regions in the Carpathian Basin), there is a high risk that they become more abundant, hindering or completely inhibiting regeneration processes. In such cases, active management is necessary to combat the invasive plants.

Acknowledgement

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SOME NOTES ON THE TOOL-USING BEHAVIOUR OF THE ANT, *APHAENOGASTER SUBTERRANEA* (HYMENOPTERA: FORMICIDAE)

G. Lőrinczi

Abstract. Ants of the genus *Aphaenogaster* lack the ability to ingest and carry large volumes of liquid food and share it through trophallaxis with other colony members in the nest. Nevertheless, these species have developed a complex method to compensate for these deficiencies by using small objects as tools to transport liquid food back to the colony. In the present study, I investigated the tool-using behaviour of *Aphaenogaster subterranea* in retrieving food through field observations using honey and petroleum jelly baits. Similarly to other members of its genus, the tool-using behaviour of the foraging workers of *A. subterranea* consisted of three distinct components at honey baits, dropping tools into the liquid food, adjusting the position of tools brought by other workers, and transporting the food-soaked tools back to the colony. The proportion of tool-using workers constituted only a small fraction of the total number of workers that were observed at baits, however, the number of workers manipulating tool items was positively correlated with the number of workers performing other activities. Materials most commonly used as tools were particles of soil and easily moveable, broken fragments of plant materials (e.g., bits of pine needle, cone and bark). Tool-using workers also dropped some debris into petroleum jelly, a non-food substance presenting a potential hazard of drowning or becoming entangled, at 60% of the baits, however, at a significantly lower intensity than in the case of honey. Adjusting or removing tool items soaked with petroleum jelly, on the other hand, was never observed.

Key words: Aphaenogaster subterranea, food transport, foraging, tool use.

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Introduction

Tool use, according to St. Amant and Horton's (2008) definition, is "...the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment". Although the most diverse forms of tool-using behaviour are a characteristic of passerine birds and primates, the occurrence of tool use is fairly widespread in animals, and it has been described in members of eight classes in three phyla (Mollusca:

Gastropoda, Cephalopoda, Arthropoda: Malacostraca, Arachnida, Insecta, Chordata: Actinopterygii, Aves, Mammalia) (Bentley-Condit and Smith 2009).

In ants, one of the most well-known forms of tool use occurs among weaver ants of the genera *Oecophylla, Polyrhachis* and *Camponotus*. These ants build their nests made of leaves stitched together using the silk produced by their larvae, which are held and manipulated by workers during nest construction (Hölldobler and Wilson 1990). Other species, such as *Dorymyrmex bicolor* or *Aphaenogaster cockerelli* use small stones and other objects to plug the nest entrances of their competitors (Möglich and Alpert 1979, Barton *et al.* 2002.). Lin (1964-65) described a similar behaviour in *Tetramorium caespitum* (recently *Tetramorium* sp. E, cf. Steiner *et*

al. 2008), whose workers used sand grains while attacking a halictine bee, *Lasioglossum zephyrum*.

The third form of tool use exhibited by ants is when foraging workers drop debris (e.g., particles of soil, bits of leaf, etc.) into liquid food, and then transport the food-soaked tools back to the colony. This type of behaviour is a characteristic of *Aphaenogaster* species, and has been described for eight species of this genus (Fellers and Fellers 1976, Tanaka and Ono 1978, Fowler 1982, McDonald 1984, Agbogba 1985, Cerdá *et al*. 1988, Banschbach *et al*. 2006), but it also occurs in *Pogonomyrmex badius* (Morrill 1972) and *Solenopsis invicta* (Barber *et al*. 1989). In *Aphaenogaster* species, liquid food is utilized more efficiently by tool use than by internal transport; furthermore, this behaviour may increase the ability of these species to compete more successfully with other ant species (Fellers and Fellers 1976, Tanaka and Ono 1978).

In this study, I investigated the tool-using behaviour of *Aphaenogaster subterranea* in retrieving food through field observations, and attempted to answer the following questions: (1) What types of behaviour patterns do tool-using workers exhibit? (2) What is the ratio of workers that perform these tasks? (3) What types of tools are used? (4) Are there any differences in reaction of tool-using workers to liquid food and to non-food viscous liquids that present a potential hazard of drowning or becoming entangled?

Materials and methods

Study species

Aphaenogaster subterranea (Latreille, 1798) is a widely distributed Mediterranean myrmicine ant, which occurs in Central and Southern Europe, Moldova, Southern Ukraine, Crimea, Asia Minor and the Caucasus (Kutter 1977, Czechowski *et al*. 2012). It is a highly thermophilous species, inhabiting mostly moderately wet and warm deciduous forests and forest edges (Kutter 1977, Seifert 2007, Czechowski *et al*. 2012), but also occurs in pine forests (Garrido *et al*. 2002, Lőrinczi 2008, 2011, Castracani *et al*. 2010) and occasionally in dry grasslands (Csősz *et al*. 2002, Dekoninck *et al*. 2007, Seifert 2007). It nests under stones, in the soil, leaf litter and occasionally inside and/or under fallen branches (Seifert 2007, Lőrinczi 2011, Stukalyuk and Radchenko 2011, Czechowski *et al*. 2012). Colonies are monogynous and range in size from several hundred to several thousand workers (Schmid-Hempel and Crozier 1999, Seifert 2007, Stukalyuk and Radchenko 2011, Czechowski *et al*.

2012). It is an omnivorous ant, and like other species in the genus *Aphaenogaster*, also uses tools (e.g., particles of soil, bits of leaf, etc.) to transfer liquid food back to the colony (Agbogba 1985, Lőrinczi pers. obs.). Nuptial flights are from the end of July to the beginning of September (Seifert 2007). Although *Aphaenogaster* species are generally classified as opportunists using Andersen's (1995, 1997, 2010) functional group scheme (e.g., Wike *et al*. 2010), *A subterranea*, contrary to Castracani *et al*.'s (2010) classification, is categorized as cryptic by Gómez *et al*. (2003).

Study area

Field work was carried out in the pine forest on the south-facing slope of Mogyorós-hegy (Mogyorós Hill), located in the middle of the Balaton Uplands in mid-western Hungary (latitude N 47° 05' 47.22", longitude E 18° 01' 29.52", altitude 220 m, dip angle 5-10°). The climate in this region is mild, with a mean annual temperature of 10-15 ºC and mean annual precipitation of 650-700 mm (Füleky *et al*. 2007). The vegetation in the study area is predominantly composed of planted black pine (*Pinus nigra*) stands mixed with young deciduous trees, mostly manna ash (*Fraxinus ornus*).

Field work

The tool-using behaviour of *A. subterranea* in retrieving food was assessed using bait experiments on four days in August 2013. For baiting, four sets of baits, separated by ca. 15 m were randomly located. Each set consisted of five baits placed on the ground along a line transect at 3-m intervals. Baits were plastic discs (8 cm in diameter) (see Fig. 5) with a quarter-teaspoon of honey and petroleum jelly as bait substances placed ca. 5 cm apart from each other. Petroleum jelly was used to test the hypothesis whether debris dropping also functions to protect workers from drowning or becoming entangled in non-food viscous liquids.

On each day of the experiment, the number, localization and behaviour of foraging workers at baits were recorded every 20 minutes for four consecutive hours from 6:20 am to 10:20 am. During each 1-minute observation period, the following behaviour patterns were distinguished: (1) feeding on bait substances ("feeding"); (2) being present at baits without any significant activity ("present"); (3) dropping tools into bait substances ("dropping"); (4) adjusting the position of tools ("adjusting"); (5) transporting food-soaked tools from the bait back to the colony ("transporting").

Results

During the experiment, the most abundant and frequent ant species recorded in the study area was *A. subterranea*, other ants (e.g., *Temnothorax* spp., *Formica* spp., *Camponotus* spp.) occurred only sporadically at baits.

Overall, significantly more workers of *A. subterranea* were recruited to honey baits than to petroleum jelly baits (Wilcoxon signed rank test, z=9.55, p<0.001, n=123) (Fig. 1).
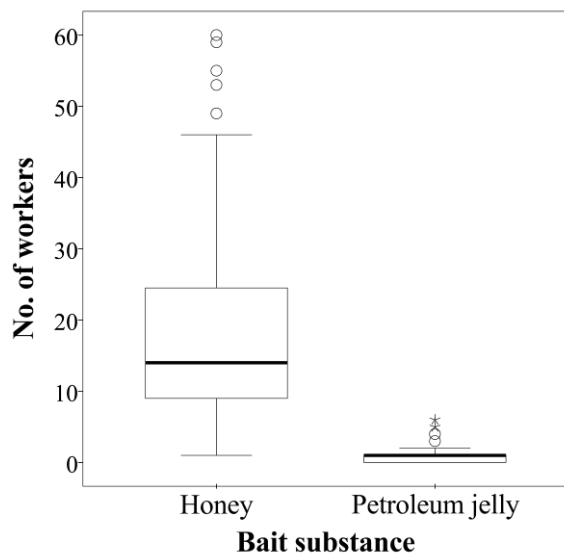

Fig. 1. Bait substance preference of the foraging workers of *Aphaenogaster subterranea*. Boxes indicate the interquartile range; horizontal lines in the boxes indicate the medians; whiskers include all points to 1.5 times the interquartile range; open circles indicate outliers; asterisks indicate extreme outliers.

The tool-using behaviour of foraging workers visiting honey baits consisted of three distinct components that were usually performed by different individuals: (1) selecting, picking up, carrying and dropping tools into the liquid food until its surface was entirely covered; (2) adjusting the position of tools brought by other workers in order to be soaked fully with food; (3) removing and transporting food-soaked tools from the bait back to the colony. In one case, however, it was observed that a worker did not drop the carried tool item into the food, but started to dip it, and then immediately transported it away.

Although the number of workers manipulating tool items was significantly lower than the number of workers performing other activities (Wilcoxon signed rank test, z=9.41, P<0.001, n=123) (Fig. 2), there was a positive correlation between them (Spearman's correlation test, r=0.54, p<0.001,

n=123), i.e., the more workers visited the baits, the more exhibited some form of tool-using behaviour.
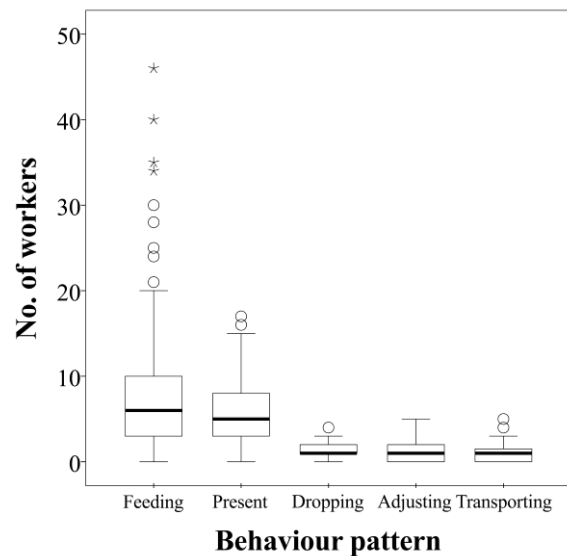

Behaviour pattern

Fig. 2. Behaviour patterns exhibited by the foraging workers of *Aphaenogaster subterranea* at honey baits. Boxes indicate the interquartile range; horizontal lines in the boxes indicate the medians; whiskers include all points to 1.5 times the interquartile range; open circles indicate outliers; asterisks indicate extreme outliers. /"feeding"/: feeding on honey; /"present"/: being present at baits without any significant activity; /"dropping"/: dropping tools into honey; /"adjusting"/: adjusting the position of tools; (5) /"transporting"/: transporting food-soaked tools back to the colony.
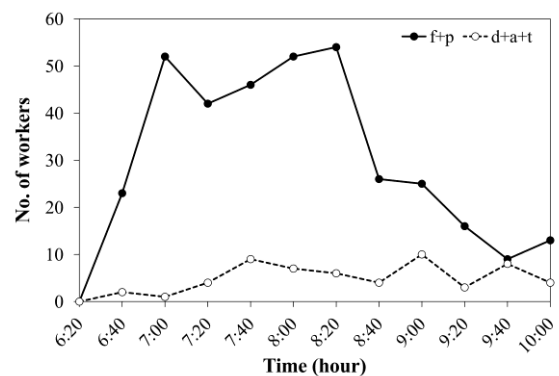

Fig. 3. Temporal dynamics of the number of foraging workers exhibiting different behaviour patterns at a honey bait in the case of one of the studied colonies of *Aphaenogaster subterranea*. /f+p/: feeding workers and workers being present at the bait without any significant activity ("feeding" + "present"); /d+a+t/: tool-using workers ("dropping" + "adjusting" + "transporting").

In the case of the more active colonies of *A. subterranea*, which recruited a larger number

(>40) of workers to baits, the number of workers manipulating tool items remained relatively constant during the survey period, while the number of workers performing other activities decreased shortly after an initial increasing and saturation (Fig. 3).

Although petroleum jelly was usually ignored by visiting workers, it provoked a fleeing or offensive reaction from some individuals after a short antennation. In addition, workers dropped some debris into petroleum jelly at 60% of the baits, however, at a significantly lower intensity than in the case of honey (Wilcoxon signed rank test, z=8.41, P<0.001, n=123) (Fig. 4). Adjusting or removing tool items soaked with petroleum jelly, on the other hand, was never observed.
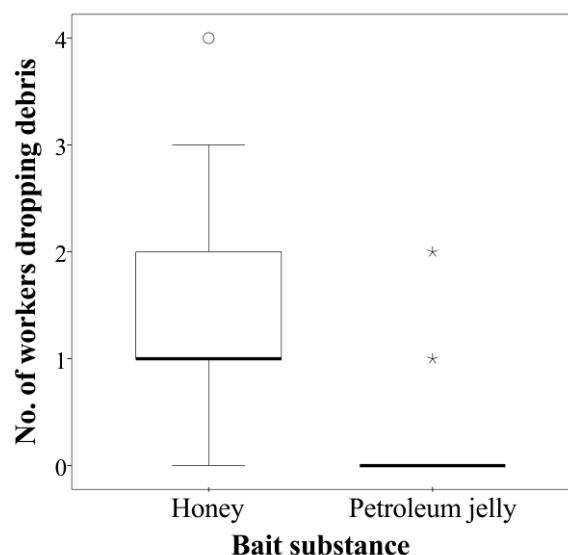

Fig. 4. The number of foraging workers of *Aphaenogaster subterranea* serving as debris droppers in the presence of the two types of bait substances. Boxes indicate the interquartile range; horizontal lines in the boxes indicate the medians; whiskers include all points to 1.5 times the interquartile range; open circles indicate outliers; asterisks indicate extreme outliers.

The types of tools used by foraging workers of *A. subterranea* varied somewhat from colony to colony. Particles of soil and easily movable, broken fragments of plant materials (e.g., bits of pine needle, cone and bark) were used most commonly, which were collected directly from the side of the baits. Tools were mostly carried by single workers, although in some cases, the larger, food-soaked items were transported cooperatively by two workers.

Discussion

Contrary to the members of the subfamilies Formicinae and Dolichoderinae, which possess a greatly distensible crop and a highly modified proventriculus allowing them the storage of large volumes of liquid food (Eisner and Brown 1958, Davidson *et al.* 2004), *Aphaenogaster* species, like other members of the subfamily Myrmicinae, lack these adaptations. In the case of *Aphaenogaster rudis*, for instance, the quantity of liquid food carried by an ant is only 10% of its original body weight (Fellers and Fellers 1976), while in the case of the syntopic formicine species, *Prenolepis imparis*, the extent of weight gain could reach an average of 130-200% (Lynch *et al.* 1980). In addition, the members of some genera in the subfamily Myrmicinae (e.g., *Aphaenogaster, Messor, Pogonomyrmex*) perform no trophallaxis (Agbogba 1985), a process by which other ant species exchange liquid food stored in their crops between members of a colony through regurgitation (Hölldobler and Wilson 1990). Tool use, therefore, may have evolved in these species to compensate for their inability to ingest and carry large volumes of liquid food and share it through trophallaxis with other colony members remaining in the nest. During this behaviour, foraging workers drop debris (e.g., particles of soil, bits of leaf, etc.) into the liquid food, and then transport the food-soaked tools back to the nest, where other workers lick the food from them (Fellers and Fellers 1976, Agbogba 1985).

This particular type of behaviour has been documented for eight species of the genus *Aphaenogaster* (Fellers and Fellers 1976, Tanaka and Ono 1978, Fowler 1982, McDonald 1984, Agbogba 1985, Cerdá *et al.* 1988, Banschbach *et al.* 2006), including *A. subterranea*, although in the case of the latter, only in laboratory colonies (Agbogba 1985). As was pointed out by Fellers and Fellers (1976) and McDonald (1984), this behaviour may have evolved from the tendency shown by many ant species to cover immovable, disagreeable substances (i.e., that present a potential hazard of drowning or entanglement to workers) near the nest with various types of debris particles, sometimes in sufficient amount to bury them completely (Wheeler 1910). This may explain why debris dropping behaviour is released more readily by the lower viscosity of the food (Tanaka and Ono 1978).

While in the study of Banschbach *et al.* (2006), *A. rudis* placed debris on 63-94% of the liquid food baits that it visited, debris dropping by *A. subterranea* was observed in all cases at honey baits, without any exception, in this study. Debris dropping

usually began shortly after the baits were discovered, even if the tool-using workers had to crawl over the backs of feeding workers surrounding the food. The bits of debris were first placed around the periphery of the honey droplets, but subsequently building inwards until their entire surface was covered.

Similarly to other members of its genus, the tool-using behaviour of *A. subterranea* consisted of three distinct components (i.e., dropping, adjusting and transporting tools) that were usually performed by different individuals. In one case, however, a worker was observed that did not drop the carried tool item into the food, but started to dip it, and then immediately transported it away. Such a particular form of tool-using behaviour has not been documented even in the case of the well-studied *A. rudis* (Banschbach, pers. comm.), which raises the question of whether this behaviour represents a species-specific trait or its occurrence is too rare to be detected by similar studies.

Contrary to the fact that the number of workers manipulating tool items was positively correlated with the number of workers performing other activities, the proportion of tool-using workers constituted only a small fraction of the total number of workers that were observed at baits. This is
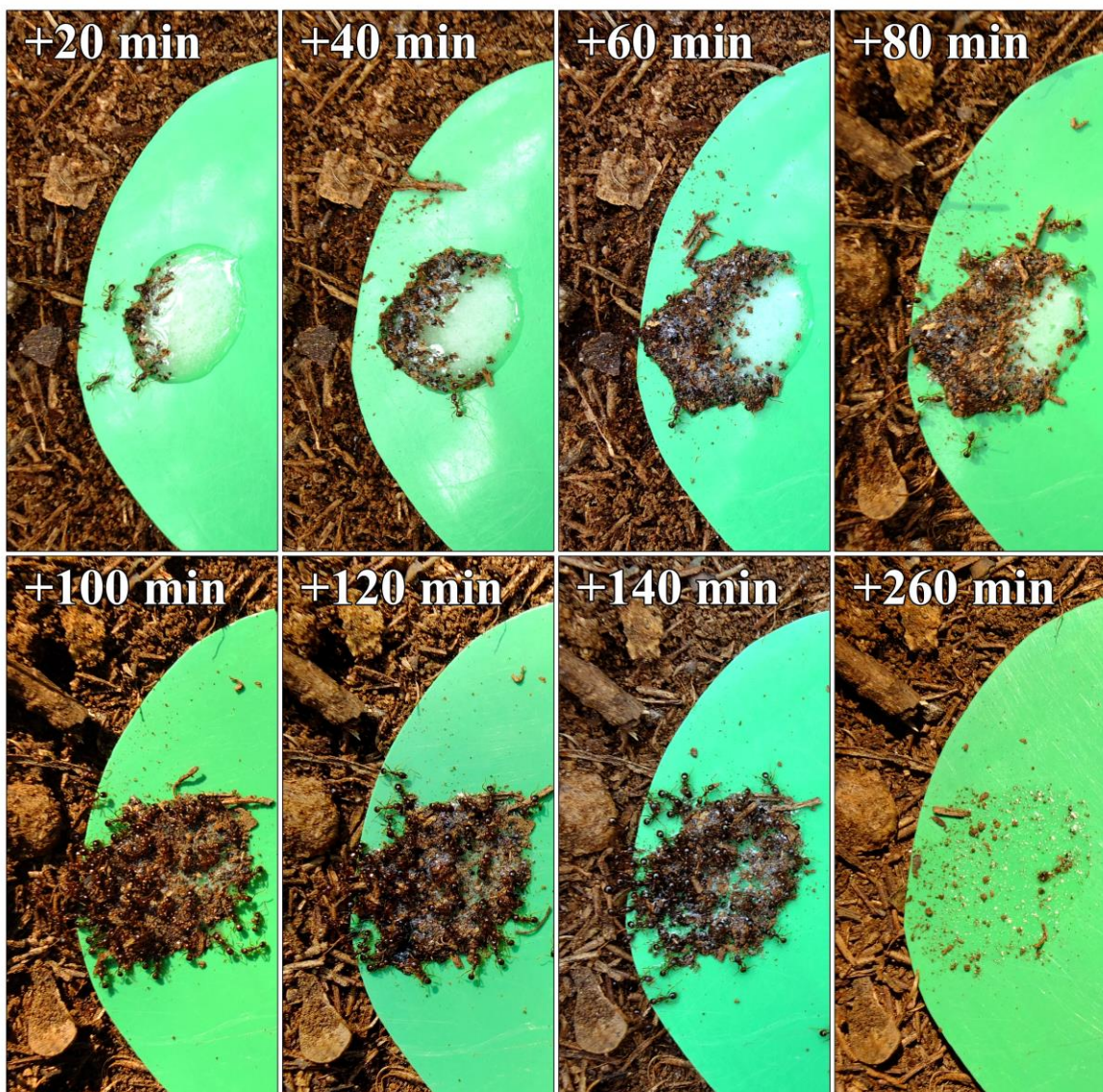

Fig. 5. Time course of honey removal by the tool-using workers of *Aphaenogaster subterranea* following the placement of baits.

consistent with the study of Banschbach *et al.* (2006), who demonstrated that tool-use represents a specialized task performed by a small subset of foraging workers of *A. rudis*, regardless of the size of the colony. The efficiency of the tool-using workers of *A. subterranea* was well shown in the case of the more active colonies, where tool-using workers, despite their small number, were able to transport almost all of the food available from the bait back to the colony in only a few hours (Fig. 5).

After a short searching time, the foraging workers of *A. subterranea* that served as debris droppers picked up tools that were nearest to the baits, and were the most easily movable. As was demonstrated in laboratory colonies of *Aphaenogaster famelica* and *A. rudis*, tool-using workers did show preference for certain tool items, which may be related to the ease of their manipulation or to the amount of food that can be absorbed or adhere to their surface (Fellers and Fellers 1976, Tanaka and Ono 1978). Nevertheless, in the natural habitats of *Aphaenogaster* species, the occurrence and availability of different potential tool items may also be important factors (Fellers and Fellers 1976).

One of the major adaptive advantages of tool use in retrieving food is that foraging workers are capable to transport much larger quantities of liquid food by tools than by direct, internal transport. For instance, by using tools, a worker of *A. rudis* is able to carry an amount of food approximately equalling its body weight (Fellers and Fellers 1976), while the amount of food carried by a worker of *A. famelica* is about 1.5-3.5 times its body weight (Tanaka and Ono 1978). The foraging activity of tool-using workers, and consequently the amount of food transported back to the colony, however, can be influenced by factors such as the size of the colony (McDonald 1984, Banschbach *et al.* 2006), the food demands of the colony (McDonald 1984, Barber *et al.* 1989, Banschbach *et al.* 2006) and the presence/absence of the foundress queen (Agbogba 1985).

In addition to a more effective utilization of liquid food, tool-use may increase the ability of *Aphaenogaster* species to compete more successfully with other ant species. By using tools, foraging workers do not need to spend a considerable time at the food source, so they can minimize interference with behaviourally dominant ant species that actively exclude subordinate species from food sources. For instance, in the study of Fellers and Fellers (1976), the workers of *A. rudis* dropped tools into the liquid food even in the presence of dominant ant species, and then returned later to retrieve the food-soaked tools once the dominant species leaved, thereby

taking a lower risk than in the case of continuous feeding. In addition to other strategies employed by subordinate ant species (e.g., enhanced ability to find food sources, high thermal tolerances, avoidance behaviour, etc.), tool use may represent another method that allows these species to utilize food sources from which they would be otherwise excluded (Fellers and Fellers 1976). Furthermore, debris dropping may discourage other ants from visiting food sources that had been previously colonized by the tool-using species (Fowler 1982, Banschbach *et al.* 2006.). Since *A. subterranea* can be considered as an ecologically dominant species in the study habitat, being capable of monopolizing most of the baits (Lőrinczi, not published), the above discussed "stealthy behaviour" exhibited by the tool-using workers of *A. rudis* was not observed either in the present or in previous studies. Nevertheless, similarly to *A. rudis*, the foraging workers of *A. subterranea* began debris dropping even in cases when other species were present at the baits. Furthermore, in another study, *A. subterranea* was observed to be able to protect honey baits that had been fully covered with bits of debris against highly aggressive species like *Liometopum microcephalum* (Lőrinczi, pers. obs.).

At more than half of the baits, the foraging workers of *A. subterranea* dropped debris into the petroleum jelly, however, at a much lower intensity and quantity than in the case of honey. In the field study of McDonald (1984), a similar reaction was observed for *Aphaenogaster albisetosa*, whose workers regularly dropped pebbles and sand not only into honey water, but into distilled water, however, only up to a few meters from their nests. In contrast, in laboratory colonies of *Aphaenogaster senilis* and *A. subterranea* (Agbogba 1985), as well as *A. rudis* (Banschbach *et al.* 2006), workers were never observed dropping debris into non-food substances such as water or petroleum jelly, despite the proximity of these substances to their nests. This suggests that debris dropping as a general response to non-food viscous liquids that present a potential hazard of drowning or entanglement to workers may be highly species and/or context dependent.

Of course, the question arises when and how frequently do *Aphaenogaster* species exhibit tool use under natural conditions. Banschbach *et al.* (2006) found that potential tools (e.g., pieces of leaf and bark, clumps of dirt, etc.) represented a small, but non-negligible percentage of the items carried by the workers of *A. rudis* returning to their nests while no artificial food sources were available to the ants. Furthermore, in the laboratory experiments of Fellers and Fellers (1976) and Agbogba (1985), the workers

of different *Aphaenogaster* species used tools to gather the body fluid of dead arthropods in the same way they had with the jelly or honey. All of these findings suggest that this particular form of behaviour is exhibited not only in the presence of artificial carbohydrate-rich food sources (e.g., honey water) and/or under laboratory conditions, but is an integral part of the natural foraging strategy of these species.

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bord-ER — COMPUTER PROGRAM FOR PERFORMING MOVING SPLIT-WINDOW ANALYSIS

L. Körmöczi and Cs. Varró

Abstract. Vegetation ecologists and soils scientists frequently use moving split-window analysis for partitioning transect data, and reveal boundaries. Few existing softwares supported this research activity, but non of them was equipped with statistical significance test. A new software was developed to mitigate this shortcoming. We offer a user-friendly tool with five distance/dissimilarity functions and two types of random reference. This paper is a short description of the program.

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Introduction

Moving split-window (MSW) analysis is frequently used in soil and vegetation pattern analysis. It is very efficient in revealing discontinuities (boundaries) in one dimensional data sets. User friendly software, however, is not available that may compute the confidence limits for significance test. We intended to fill this gap, and provide an easy to use application for MSW

Softwares for MSW-computations

The computation of dissimilarity metrics in the MSW analysis is not a big challenge, it can be performed even with a spreadsheet software. This works well with a single window width, but dealing with multiple window widths and handling randomized data are rather difficult in such a way. The PASSaGE software also contains the computation of a dissimilarity profile (Rosenberg and Anderson, 2011). This software package is declared as "a free, integrated, easy-to-use software package for performing spatial analysis and statistics on biological and other data". Though it may compute dissimilarities for several window sizes the statistical significance is missing. Computations can be done in the R environment. For example, the software of Rossiter (2013) enables to carry out MSW analyses using multiple window widths and it offers two dissimilarity indices. However, it does not offer any randomizations.

We developed earlier our own software in the statistical language R (version 2.10.1, www.R-project.org). This is equipped with random references, and computes upper confidence limits but the runtime is rather long (Erdős et al. 2014b). Therefore the new version of the software has been written in C, and compiled with QT Creator.

Installation

The software is freely downloadable from http://expbio.bio.u-szeged.hu/ecology/kormoczi/ bordER/index.html

The installation of **bord-ER** is easy: Just download the file 'bordER.exe' and put it anywhere on your harddisk. Double-clicking the file will start the program. Windows will consider this a breach of security, and will ask if you trust the software provider. If you want to use the program, you will have to answer yes.

The lack of "formal" Windows installation is intentional, and allows installation without administrator privileges.

bord-ER is a stand-alone program to perform moving-split window analysis with various dissimilarity indices. It gives confidence limits for statistical significance of deviation from random distribution.

The procedure known as Moving Split-Window Analysis is designed to reveal discontinuities in one-dimensional sequential data set on the basis of dissimilarity values of neighbourhoods. Sequential data set may be any regular sequence of univariate or multivariate data vectors. In ecology it is often used on regular samples of transect data. Increasing window width results in a kind of spatial scaling. Significance test of this statistic is based on the random distribution of attribute values.

Input data structure

Input data must be arranged in an ASCII file (as that comes from EXCEL). Tab, comma, semicolon or space are accepted as field delimiter. Data should be either integer or real numbers. Only decimal point (.) are accepted as decimal separators. Sequential data vectors are arranged in rows: rows are the sequential sampling units, and columns are the variables. No row or column headers are used. Sample data structure can be found in `sample.txt` that is also available at the homepage of the software.
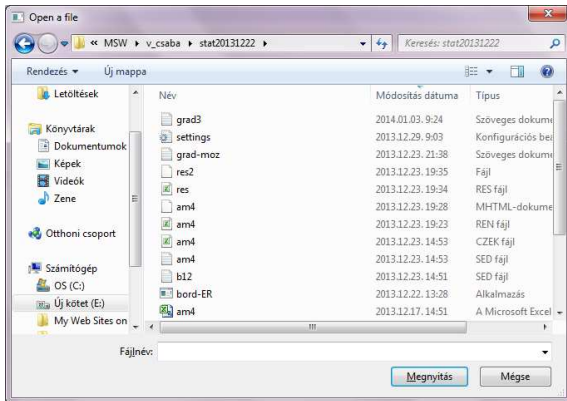
Performing the analysis

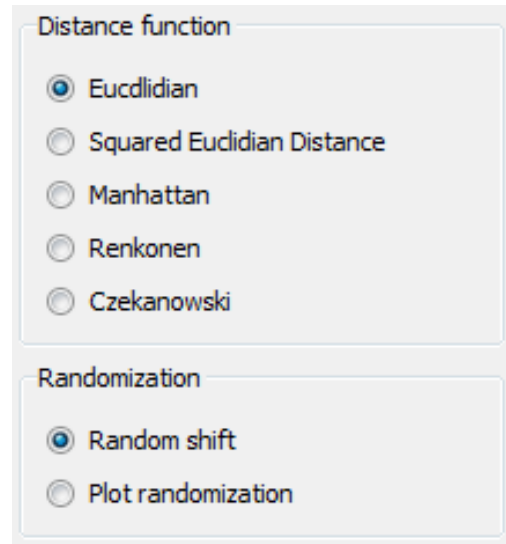Double-clicking the program name opens the following window:
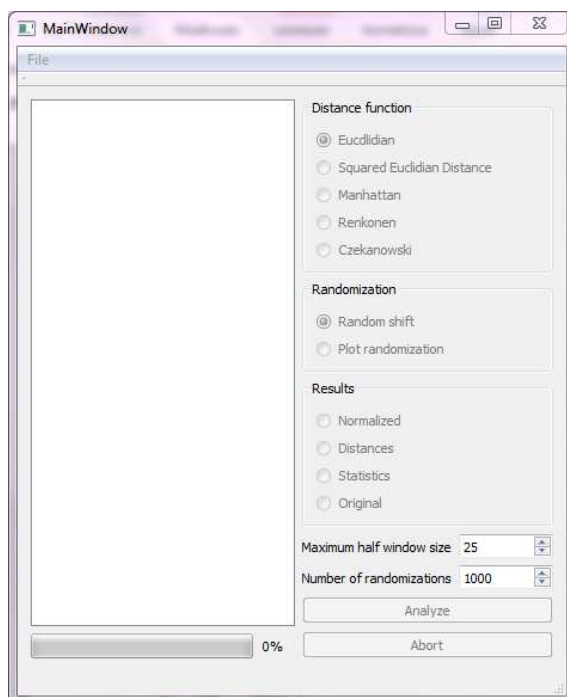
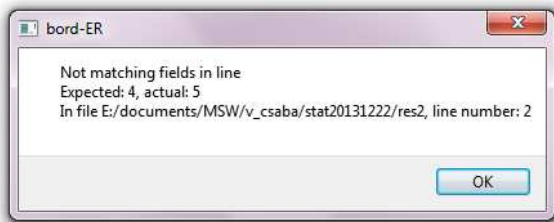"File" dropdown list contains "Open", "Save" and "Exit" commands.
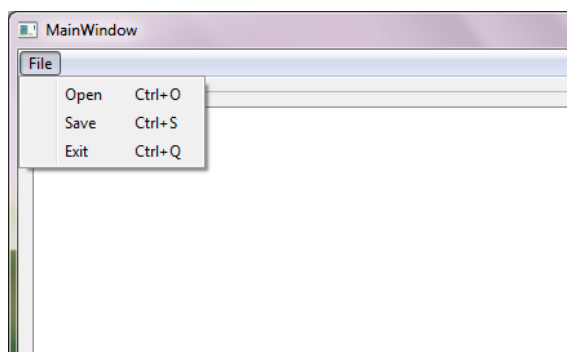
Clicking "Open" you can search for the desired file in the usual browser window. You can open only matching files,

otherwise an error message appears.

If an appropriate file is open, the raw data appear in the MainWindow in tabular form, and the following options can be chosen:
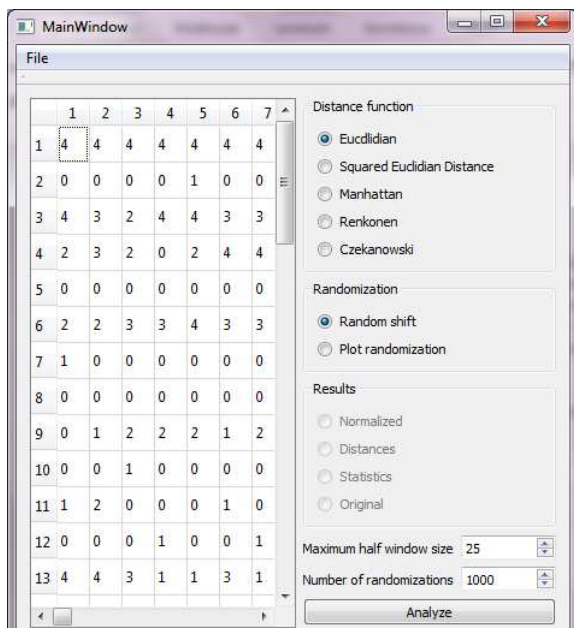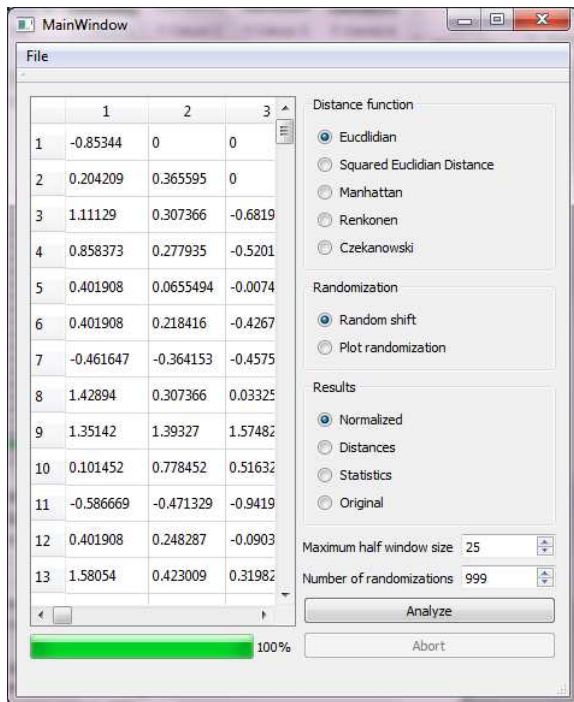

One of the five distance/dissimilarity functions can be chosen at the right panel. Two types of randomization is implemented in the program, but the use of Random shift is suggested.

You may set the Maximum half-window size (by default: 25) and the number of Random iterations (by default: 999). The last set of these values is saved in settings.ini file, and is used in the next run of the program.

Clicking the Analyze button starts the analysis with actual settings; a process indicator shows the state of analysis. The resulted values can be checked in three windows:

Results: Normalized option window shows the Z-scores of actual running for each half-window size. Those data are for drawing dissimilarity profiles.

Results: Distances option window shows the dissimilarity/distance values for each half-window sizes in the scale of the dissimilarity function applied.
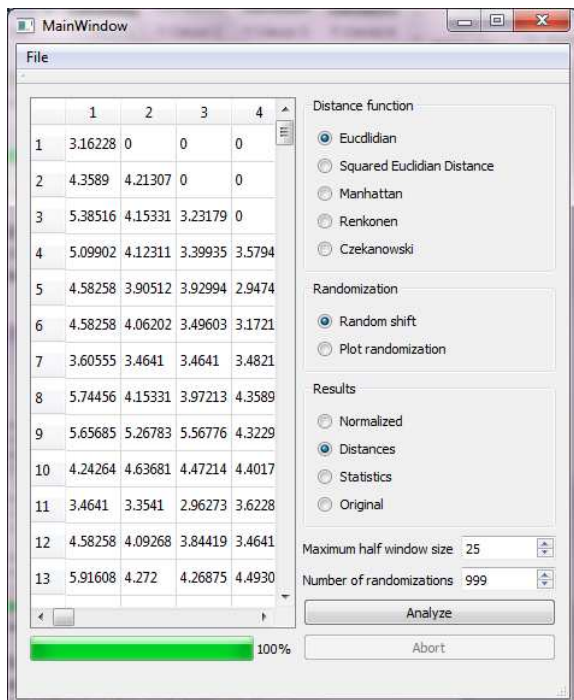
Results: Statistics window displays the overall mean and standard deviation of dissimilarity values of the random reference for each half-window sizes. Also 10 %, 5 %, 2.5 % and 1 % confidence limits are listed.
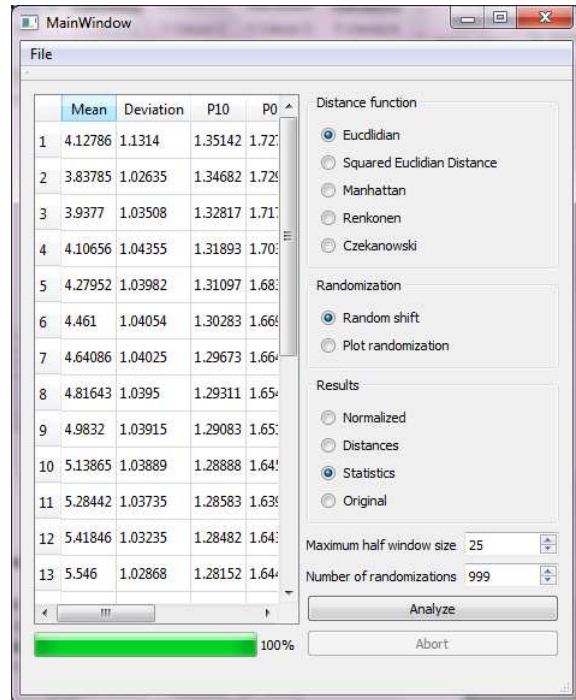
File: Save option saves all of the results in a tab delimited file of specified name. (Important! In the present state the software does not save the results in a directory the name of which contains special characters!) Statistics, original dissimilarity values and Z-scores are saved. Header of the data sequence contains the details of the analysis.

Moving split window analysis
Maximum window size range: 25
Randomization count: 999
Row number:48
Species number: 220
Comparative function: Euclidean distance
Random reference with: Random shift of species

Saved file should be opened in Excel or other spreadsheet application, and dissimilarity profiles should be drawn as appropriate. Dissimilarity profiles are drawn from Normalized (Z-score) data, either for each window size or an average Z-score over several window sizes. Averaging should be done in the spreadsheet application. Level of

significance can be drawn on the basis of confidence limits as is shown below.
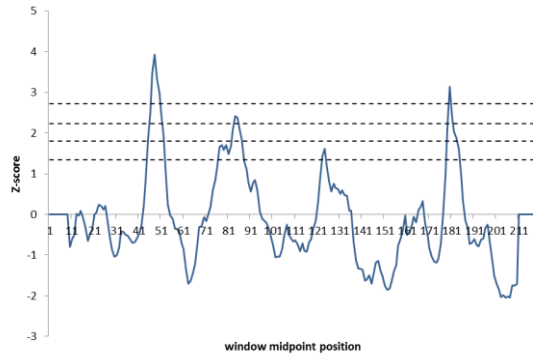
Computation

On the basis of Cornelius and Reynolds (1991), the description of MSW-technique is the following (with some comments and improvement). Consider a data series of $j = 1, 2, 3, ... m$ ordered positions with $i = 1, 2, 3, ... n$ measurement variables at each position. Mostly belt transects consisting of contiguous or evenly placed quadrats are used in community composition measurements. x_{ij} is the abundance of the ith variable at the jth position along the series. Consider a window of width q that brackets sequential positions along the series. q is a non-zero, even integer expressed in the measure of the sampling units, $q < m$. A window of width q is split into two equal halves, designated by W_A and W_B. A series of length m will have $m-q+1$ sequential overlapping windows of width q, where the location of each window midpoint is $r + 0.5$, where $r = q/2$, $q/2 + 1$, $q/2 + 2$, ... $m-q/2$. For each window midpoint location each variable i is averaged in each window half. A dissimilarity/distance index can be calculated between each of the $m-q+1$ pairs of average vectors. Any dissimilarity or distance index can be used.

The following marks are used in the index descriptions. $D_{j,j+1,k}$ is the dissimilarity value at the $j+0.5$-th window midpoint position, for half-window size k; n is the number of variables; m is the length of data series; $j=k,k+1,...,m-k$, $k=1,2,...,m/2$; k is the half-window width; $x_{i,j,k}$ is the abundance of i-th variable at the j-th position along the data series averaged for the half-window size k.

Euclidean distance:

$$EUC_{j,j+1,k} = \sqrt{\sum_{i=1}^{n}(x_{i,j,k} - x_{i,j+1,k})^2}$$

Squared Euclidean distance:

$$SED_{j,j+1,k} = \sum_{i=1}^{n}(x_{i,j,k} - x_{i,j+1,k})^2$$

Manhattan metric:

$$M_{j,j+1,k} = \sum_{i=1}^{n}|x_{i,j,k} - x_{i,j+1,k}|$$

Complement of Renkonen index:

$$DREN_{j,j+1,k} = 1 - \sum_{i=1}^{n} min\left\{\frac{x_{i,j,k}}{\sum_i x_{i,j,k}}, \frac{x_{i,j+1,k}}{\sum_i x_{i,j+1,k}}\right\}$$

Complement of Czekanowski index:

$$DCZ_{j,j+1,k} = 1 - \frac{2\sum_{i=1}^{n} min(x_{i,j,k}, x_{i,j+1,k})}{\sum_{i=1}^{n}(x_{i,j,k} + x_{i,j+1,k})}$$

Expected mean dissimilarity/distance and standard deviation (SD) can be calculated from dissimilarity/distance values that are revealed from n-times randomized data with the same procedure as that in the previous paragraph. Expected mean and standard deviation for a given window width are calculated as the mean and SD of all data. Any kind of randomization can be used but we tested complete randomization and two restricted randomizations: random repositioning the plots and random shift of species.

Overall mean dissimilarity and SD are used in Z-transformation according to Cornelius and Reynolds (1991):

$$Z_{j,j+1,k} = \frac{D_{j,j+1,k} - \overline{D_{exp,k}}}{SD_{exp,k}}$$

where $D_{exp,k}$ is the overall mean and $SD_{exp,k}$ is the sdandard deviation of dissimilarities from random reference for half-window width k.

Randomization

Reference distribution for statistical tests is given by permutation procedure. Two kinds of randomization are implemented in the programme: an unrestricted randomization – plot randomization, and a restricted one – random shift (c.f. Erdős et al, 2014a).
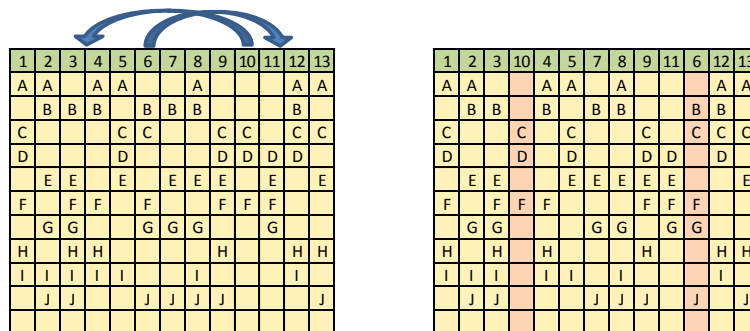
Random shift

During random shift, data belonging to the same variable are randomly shifted along the transect. Values shifted beyond the end of the transect are wrapped back on to the opposite end.
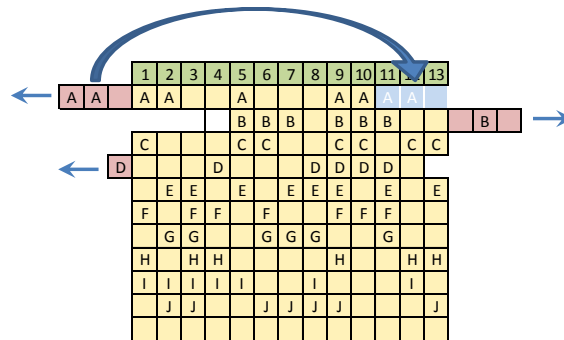
Plot randomization

Each plots is randomly repositioned along the transect.

References

Cornelius, J.M., Reynolds, J.F. (1991): On determining the statistical significance of discontinuities with ordered ecological data. – Ecology 72: 2057-2070.

Erdős, L., Bátori, Z., Tölgyesi, Cs., Körmöczi, L. (2014a): The Moving Split Window (MSW) analysis in vegetation science – an overview. - Applied Ecology And Environmental Research 12: 787-805.

Erdős, L., Zalatnai, M., Bátori, Z., Körmöczi, L. (2014b): Transitions between community complexes: a case study analysing gradients through mountain ridges in South Hungary. – Acta Botanica Croatica 73: 63-77.

Rosenberg, M.S., Anderson, C.D. (2011): PASSaGE: Pattern Analysis, Spatial Statistics and Geographic Exegesis. Version 2. – Methods in Ecology and Evolution 2: 229-232.

Rossiter, D. G. (2013): Technical note: Optimal partitioning of soil transects with R (http://www.css.cornell.edu/faculty/dgr2/teach/R/R_OptPart.pdf)