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**Druhová bohatost a variabilita cévnatých rostlin,
mechorostů a měkkýšů na vlhkostním gradientu**

Disertační práce

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Abstrakt

Luční prameniště patří k vzácným a chráněným biotopům středoevropské krajiny. V minulosti se jim věnovala řada autorů, avšak doposud nebyla podrobněji zkoumána v širším kontextu s okolními nelesními rostlinnými společenstvy. Proto jsem se v této disertační práci zabývala otázkou možného ovlivnění nelesních pramenišť jejich druhově bohatou sousední vegetací. V dalších studiích jsem se zaměřila na změny druhového složení a druhové bohatosti podél vlhkostního gradientu z pramenišť do sušších travinobylinných biotopů. Hodnotila jsem tři skupiny organismů s rozdílnými vlastnostmi i životními strategiemi, a sice cévnaté rostliny, mechorosty a měkkýše. Poslední studie si mimo jiné kladla za cíl zhodnotit studovaná společenstva z hlediska vybraných funkčních vlastností cévnatých rostlin ve vztahu k vlhkosti. Výzkumy probíhaly na nelesních vápnatých prameništích a přilehlých biotopech moravsko-slovenského pomezí.

Počet druhů cévnatých rostlin v prameništích koreloval s počtem druhů okolní vegetace jen v chladnější a vlhčí severovýchodní části zkoumaného území. Naopak na lokalitách jihozápadní části území byl zjištěn větší rozdíl mezi ekologickými podmínkami pramenišť a okolí a jejich počty druhů nebyly vzájemně korelovány. Důležitým faktorem, který pravděpodobně bránil pronikání druhů do pramenišť, byla vysoká specifita prostředí prameniště – srážení pěnovce a nedostatek živin, které omezují růst většiny rostlinných druhů.

Výrazné rozdíly v půdní vlhkosti (od 19 % v trávnicích do 97 % v prameništích) měly velký vliv na výměnu druhů všech tří skupin sledovaných organismů podél vlhkostního gradientu. Ačkoli změny druhového složení cévnatých rostlin, mechorostů i měkkýšů podél vlhkostního gradientu spolu navzájem korelovaly, ve změnách druhové bohatosti byl prokázán značný rozdíl. Počet druhů cévnatých rostlin vykazoval unimodální odpověď s optimumem posunutým do nižších hodnot vlhkosti. Druhová bohatost mechorostů lineárně klesala směrem k suchým trávnicím. Naopak žádná průkazná závislost vzhledem k vlhkostnímu gradientu nebyla potvrzena u měkkýšů, a to ani u počtu druhů ani u počtu jedinců.

Některé vlastnosti cévnatých rostlin byly ve zkoumané vegetaci preferovány, což potvrzuje teorii filtrování druhů stresujícím prostředím. Jedním z nich byla např. hmotnost semen, jejíž variabilita se mezi společenstvy prokazatelně měnila podél gradientu vlhkosti – v porostech byly druhy s lehkými semeny zastoupeny více než by odpovídalo náhodnému rozmístění druhů.

Abstract

Calcareous spring fens belong to one of the rarest and most threatened habitats of Central Europe. Even though many authors investigated both species composition and richness of fen vegetation in the past, no study dealing with spring fens in a wider context of their contact with adjacent treeless vegetation was published. Therefore I focus herewith on the potential effect of the surrounding species-rich grasslands on the species composition of calcareous spring fens. I explored changes of species composition and species richness along a moisture gradient from fens to semi-dry surrounding grasslands. I selected three groups of organisms with different traits and life strategies – vascular plants, bryophytes and molluscs. One of the aims of the study was to evaluate the selected vascular plant species traits in target vegetation with regard to the moisture gradient. All studies were carried out in the border area between Czech and Slovak Republics.

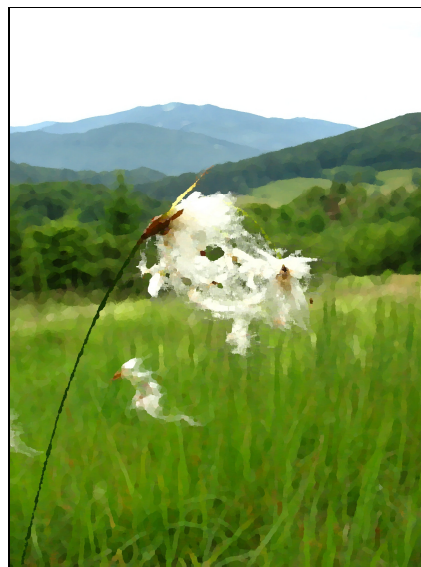
Fen species richness correlated significantly with species richness of the surrounding vegetation in the north-eastern (NE) locations, whereas no correlation was found for the south-western (SW) locations. Fens in SW locations are characterized by both intense tufa formation, which creates extreme ecological conditions, and the contrasting environmental conditions compared to surrounding grasslands.

There was a sharp moisture gradient (from 19% in semi-dry grasslands to 97% in spring fens), which influenced species composition of all three groups of organisms. Even though species composition changes of the different groups were correlated with each other, a large differences in their species richness changes were found. The relationship between number of species of vascular plants and moisture was unimodal with the optimum skewed towards lower values. For bryophytes, species richness decreased linearly towards drier plots. For molluscs, no significant response to measured soil moisture was found neither for species richness nor abundances.

Some of the species traits were preferred in our data set, which confirm the Limiting Similarity Theory. One of these traits was seed mass – its variability significantly differed along moisture gradient, and it was underdispersed with a preference of light seeds.

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Seznam článků a vymezení podílu spoluautorů

Článek I

Hettenbergerová E. & Hájek M. (2011): Is species richness of small spring fens influenced by the spatial mass effect? *Community Ecology* 12: 202–209.

EH a MH vymysleli koncept studie; EH nasbírala a analyzovala terénní data; EH a MH se podíleli na textu článku.

Článek II

Hettenbergerová E., Horsák M., Chandran R., Hájek M., Zelený D. & Dvořáková J. (2013): Patterns of land snail assemblages along a fine-scale moisture gradient. *Malacologia* 56 (v tisku).

MHo, EH a MHá vymysleli koncept studie; EH a JD nasbíraly terénní data; RCh, MHo, JD determinovali měkkýše; EH a DZ analyzovali data; EH a MHo se podíleli na textu článku, MHá, JD, DZ a RCh komentovali rukopis článku.

Článek III

Hettenbergerová E., Hájek M., Zelený D., Jiroušková J. & Mikulášková E. (2013): Changes in species richness and species composition of vascular plants and bryophytes along a moisture gradient. *Preslia* 85 (v tisku).

EH a MH vymysleli koncept studie, EH a JJ nasbíraly terénní data, EH zvažila vzorky biomasy, EH a EM determinovaly mechorosty, EH a DZ analyzovali data, EH a MH se podíleli na textu článku, DZ, JJ, EM komentovali rukopis článku.

Článek IV

Schamp B., **Hettenbergerová E.** & Hájek M. (2011): Testing community assembly predictions for nominal and continuous plant traits in species-rich grasslands. *Preslia* 83: 329–346.

BS a MH vymysleli koncept studie; EH nasbírala terénní data, získala údaje z databázi a zvažila semena chybějící v databázích; BS analyzoval data; BS, EH a MH se podíleli na textu článku.

Úvod

Půdní vlhkost

Půdní vlhkost je jednou z nejdůležitějších vlastností prostředí, které ovlivňují nejen fyziologické funkce rostlin a jejich vzhled, ale také druhové složení rostlinných i živočišných společenstev. Variabilita v druhovém složení a bohatosti rostlinných společenstev podél vlhkostního gradientu však byla v minulých letech zkoumána méně často než variabilita podél gradientu pH, produktivity nebo dostupnosti živin (např. Janssens et al. 1998, Marini et al. 2007, Cachovanová et al. 2012, Güssewell et al. 2012, Merunková & Chytrý 2012, Araya et al. 2013). Velká část prací, týkajících se gradientu vlhkosti byla publikována z příbřežních biotopů (např. Wassen et al. 2002, Loheide & Gorelick 2007) nebo lesů (např. Hutchinson et al. 1999, Kooijman & Cammeraat 2010), méně často však byla zkoumána slatiniště (např. Flintrop 1994, Hájková & Hájek 2004). Přitom právě slatiniště a jejich okolní společenstva představují vhodný biotop pro studium vlhkostního gradientu, neboť se na relativně malém prostorovém měřítku výrazně mění výška hladiny podzemní vody (Ilomets et al. 2010, Jabłońska et al. 2011). Pro studium tohoto fenoménu jsem si vybrala oblast Bílých Karpat a okolí, kde se setkávají slatiniště spolu se suchými loukami a představují tak společně unikátní, velmi dlouhý vlhkostní gradient.

Charakteristika vápnatých slatinišť

Slatinná vápnatá prameniště jsou taková místa, která jsou trvale zamokřená a mají omezenou přístupnost živin, hlavně fosforu a dusíku (Hájek & Hájková 2011). Tato místa jsou sycena převážně podzemní, minerálně bohatou vodou a často zde dochází k ukládání živin do vápnatých inkrustací (tzv. pěnovců). Vegetace je zde většinou nízká s malou produktivitou a dominují v ní mechorosty, šachorovité rostliny a jiné graminoidy. Fytcenologicky se řadí do svazu *Caricion davallianae* třídy *Scheuchzerio palustris-Caricetea nigrae*¹. Tato vegetace má rozlohu většinou jen několik málo čtverečních metrů a tvoří tak v krajině malé ostrůvky, které nejsou mezi sebou propojené. Vzhledem k velikosti a specifitě podmínek, za kterých prameniště vznikají, jsou ve střední Evropě tyto biotopy vzácné a většina z nich je chráněná zákonem. Jsou velmi náchylné k lidskému hospodaření, zejména ke změně vodního režimu způsobené odvodňováním, nebo k nadměrné eutrofizaci.

Specifické ekologické podmínky pramenišť umožňují výskyt řady vzácných a ohrožených druhů rostlin a živočichů, které jsou na ně adaptované. Z cévnatých rostlin bývají nejvýraznější charakteristické porosty suchopýrů *Eriophorum latifolium* a *E. angustifolium*, ostřic *Carex davalliana*, *C. flava* nebo orchidejí *Epipactis palustris* či *Dactylorhiza majalis*². Vzhledem k nízké dostupnosti živin a permanentní vysoké hladině podzemní vody často dominují mechorosty (Hájková & Hájek 2003), které mají velkou pokrývnost (běžně kolem 90 %). Typickými zástupci jsou vlhkomilné „nerašeliníkové“ druhy *Palustriella commutata*, *Bryum pseudotriquetrum* či *Cratoneuron filicinum*. Ze živočišné říše zde můžeme nalézt např. mezinárodně chráněné druhy měkkýšů vázané právě na pěnovcová prameniště – *Vertigo moulinsiana* nebo *V. angustior* (Horsák 2008).

Nelesní prameniště bývají obklopena různými typy travinobylinné vegetace – nejčastěji loukami (*Arrhenatherion elatioris*, *Molinion caeruleae*, *Calthion palustris*), pastvinami (*Cynosurion cristati*) nebo trávničky (*Cirsio-Brachypodium pinnati*, *Bromion erecti*, *Violion caninae*), které mohou prameniště obohacovat některými svými druhy. V těchto společenstvech výrazně převažují cévnaté rostliny nad mechorosty a porosty bývají většinou druhově bohaté (Škodová et al. 2011).

¹ Syntaxonomie je sjednocena podle Vegetace České republiky 1 a 3 (Chytrý et al. 2007, 2011).

² Nomenklatura cévnatých rostlin je sjednocena podle Seznamu cévnatých rostlin květeny České republiky (Daníhelka et al. 2012), nomenklatura mechorostů je podle Bryoflorý České republiky (Kučera et al. 2012).

Vztahy mezi biotopy

Pro porozumění ekologie jednoho biotopu je potřeba studovat celý komplex vlivů okolí, které na tento biotop působí. Je známo, že složení a druhovou bohatost vegetace mohou ovlivňovat nejen lokální faktory, jako jsou interakce mezi rostlinami a živočichy nebo abiotické podmínky (dostupnost vody, světla a živin, pH půdy aj.), ale také vlastnosti sousedních stanovišť (Dunning et al. 1992, Skov 1997, Kunin 1998). Netypické druhy se do společenstva dostávají z okolních společenstev (z tzv. *species pool*, Eriksson 1993) prostřednictvím semen či jiných rozmnožovacích útvarů a mohou po nějaký čas přežívat i v mírně nepříznivých podmínkách (tzv. *spatial mass effect*, Shmida & Wilson 1985). Zajímalo mě, do jaké míry jsou ovlivňovány tak specifické biotopy, jakými jsou prameniště. Druhového složení slatinišť se věnovala řada autorů (např. Wheeler & Giller 1982, Wassen & Joosten 1996, Hájková & Hájek 2003, Bayley & Mewhort 2004, Pouličková et al. 2005), avšak doposud nebyly podrobněji zkoumány v širším kontextu s okolními nelesními rostlinnými společenstvy.

Porovnání různých skupin organismů

Pro lepší a obecnější pochopení fungování různých ekosystémů a jejich diverzity je vhodné studovat více skupin organismů. Studium více taxonomických skupin na stejném gradientu lze zjistit, zda výsledky, které získáme pro každou skupinu zvlášť, si jsou podobné, a zda lze tedy tyto výsledky zobecnit. Vhodnou skupinou živočichů pro studium tohoto tématu jsou měkkýši. Vzhledem k jejich ekologickým nárokům a omezeným migračním schopnostem jsou svým výskytem vázáni na určité typy stanovišť. Dá se tedy (podobně jako u rostlin) mluvit o společenstvech měkkýšů. Měkkýši potřebují ke svému růstu a rozmnožování dostatečné množství vápníku, který mohou ve velké míře nalézat právě v pěnvcových prameništích. Vzhledem k tomu, že jejich měkké a drobné tělo (většinou do tří milimetrů) je náchylné k vysychání, vyhledávají měkkýši místa, která mají dostatek vlhkosti, a proto jim prameniště vyhovují i z tohoto důvodu. Naopak na vysloveně xerothermních stanovištích se téměř nevyskytují. Na většině bělokarpatských luk je jejich výskyt omezen také vlivem odvápnění horních vrstev půdy (Horsák 2008).

Podle předchozích výzkumů je možno předpokládat, že se bude druhová bohatost měkkýšů na vlhkostním gradientu výrazně měnit. Dle některých autorů stoupá počet druhů měkkýšů směrem k vlhčím místům (Wäreborn 1969, Martin & Sommer 2004a, b) nebo je nejvyšší počet druhů uprostřed gradientu (Getz & Uetz 1994). U rostlin byl potvrzen podobný unimodální trend (Hou et al. 2008), i když většina prací uvádí spíše lineární závislost stoupající směrem do sucha (např. Dwire et al. 2004, Zelnik & Čarni 2008).

Studie, týkající se více skupin organismů v souvislosti s vlhkostí prostředí nejsou hojné. Dvořáková & Horsák (2012) zjistili, že vlhkost a obsah vápníku v půdě byly nejdůležitějšími faktory, které vysvětlily nejvíce variability jak v rostlinných, tak i měkkýších společenstvech luk Bílých Karpat. Další výzkumy se spíše dotýkaly otázky gradientu minerální bohatosti mokřadních společenstev, kde korespondoval hlavní trend u měkkýšů s hlavním trendem ve vegetaci (Horsák & Hájek 2003). Vegetace totiž odráží biotické a abiotické faktory, které také ovlivňují měkkýše (např. geografická poloha, podnebí, půdní reakce apod.). Samotná struktura vegetace také ovlivňuje společenstva měkkýšů, a to dokonce více než její druhové složení (Labaune & Magnin 2001). Srovnání vztahu cévnatých rostlin, mechorostů a měkkýšů ke gradientu vlhkosti dosud nebylo publikováno. Cévnaté rostliny a mechorosty byly častěji porovnávány s ohledem na gradient pH či vápníku (Hájek et al. 2011, Sekulová et al. 2012, 2013). Srovnání těchto skupin je zajímavé, vzhledem k jejich rozdílným vlastnostem, jako je např. velikost organismu, typ reprodukce, příjem a hospodaření s živinami a vodou apod. (Kapfer et al. 2012, Street et al. 2012). Jedním z cílů této práce je proto zjistit, zda existuje podobný trend mezi cévnatými rostlinami, mechorosty a měkkýši ve vazbě na gradienty prostředí na bazických prameništích a jejich okolí.

Morfologické vlastnosti rostlin podél gradientu vlhkosti

Řada studií hledá odpověď na otázku, zda se druhy s různými vlastnostmi vyskytují v přirozeném prostředí náhodně, nebo jsou některé vlastnosti preferovány (např. Weiher & Keddy 1995, Weiher et al. 1998, McGill et al. 2006, Schamp & Aarsen 2009, Saatkam et al. 2010). Tato problematika byla studována i u měkkýšů (Schamp et al. 2010). Teorie limitující podobnosti (*Limiting similarity theory*, MacArthur & Levins 1967) předpokládá, že v určitém prostředí mohou koexistovat druhy, které se svými nikami nepřekrývají, nebo se překrývají jen částečně. Totéž by mělo platit i pro vlastnosti druhů (např. výška rostliny, váha semen, typy plodů apod.). Na druhou stranu existuje teorie, která předpokládá, že druhy, které se společně nachází v daném biotopu, prošly určitým filtrem prostředí, a mají tedy podobné vlastnosti (*environmental filtering*, Weiher & Keddy 1995). S ohledem na tyto dvě teorie jsem chtěla zjistit, jestli jsou některé z vlastností cévnatých rostlin ve studovaném území spíše náhodné nebo preferované a jak se tyto vlastnosti mění na gradientu vlhkosti.

Cíle disertační práce

Článek I

Zjistit, do jaké míry může být druhové složení slatinišť ovlivněno sousední nelesní vegetací.

Články II a III

Prozkoumat změnu v druhové skladbě a bohatosti rostlinných společenstev podél gradientu vlhkosti. Zjistit, zda existuje stejný či podobný trend mezi rostlinnými a měkkýšími společenstvy. Sledovat, jak se mění počet specialistů a generalistů cévnatých rostlin a mechorostů podél gradientu vlhkosti.

Článek IV

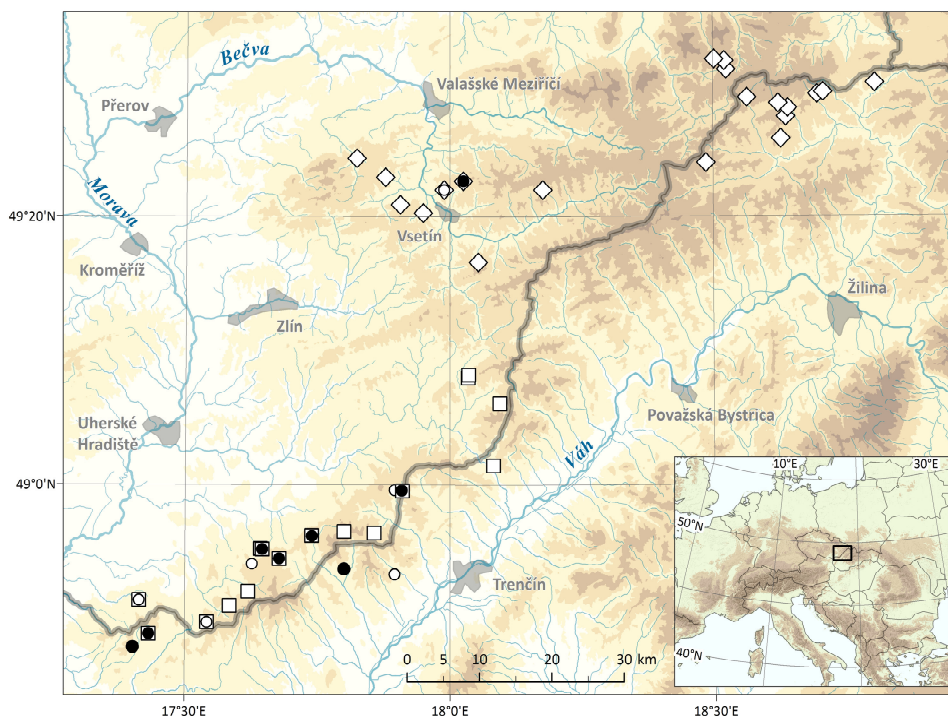
Zjistit, zda je uspořádání druhů cévnatých rostlin podél vlhkostního gradientu náhodné vzhledem k vybraným ekologickým vlastnostem jednotlivých druhů.

Metodika

Metodika každé studie je detailně popsána v jednotlivých článkách. V této kapitole bych chtěla stručně popsat sběr dat pro první studii a shrnout metodický postup, který byl z velké části společný článkům II až IV.

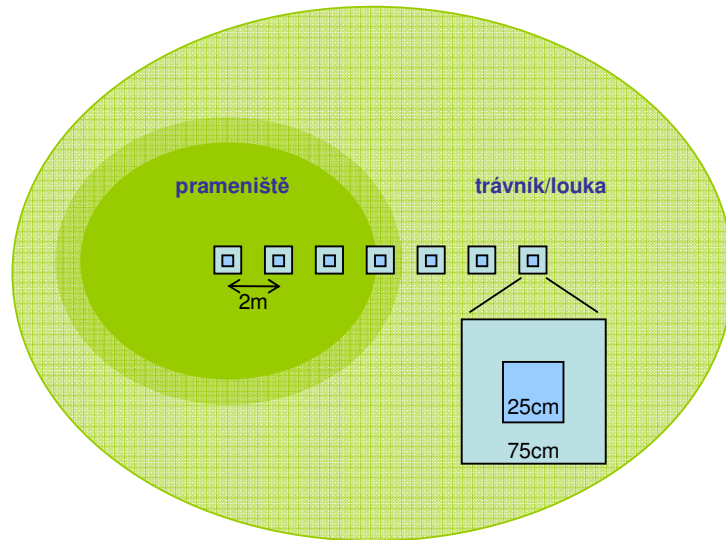
První studie, narozdíl od ostatních tří, zahrnovala slatiniště jak na větším geografickém měřítku (od Bílých Karpat až po Turzovskou vrchovinu, obr. 1), tak i na delším gradientu pH (od pěnovcových pramenišť po slatiny na nevápnitých substrátech). Celkem bylo zmapováno 36 lokalit. Na každé z nich byl na prameništi zapsán fytoocenologický snímek na ploše 16 m² a následně byly zaznamenány druhy cévnatých rostlin okolní nelesní vegetace v okruhu do 50 metrů od prameniště. Území bylo rozděleno podél geografického a klimatického gradientu na vlhčí a chladnější část severovýchodní (SV) a sušší a teplejší část jihozápadní (JZ).

Pro další tři studie byla vybrána oblast s výskytem pěnovcových pramenišť na moravské i slovenské straně Bílých Karpat a Hostýnsko-vsetínské hornatiny. Na každé lokalitě byl veden transekt vždy ze střední (nejvlhčí) části prameniště do suššího trávníku nebo louky (obr. 2). Délka transektu závisela na rozloze prameniště a jeho případného okraje ve střední části transektu. Tato okrajová plocha byla v terénu většinou dobře rozpoznatelná. V sušší části transektu byl zapsán stejný počet ploch jako v prameništi. Střední ploch byly od sebe vzdáleny vždy 2 metry. Nejkratší transekt měl pět ploch, zatímco nejdelší 16. Celkem byly zapsány snímky na 126 plochách patnácti transektů, z čehož pro malakozoologickou studii bylo použito 9 transektů se 60 plochami (obr. 1).



Obrázek 1. Přehled studovaných lokalit. Čtverce představují dvě skupiny lokalit z první studie (□ JZ a ◇ SV skupina); kolečka představují lokality II. až IV. studie, přičemž plná kolečka obsahují lokality se studovanou vegetací i měkkýši, prázdná kolečka lokality bez studovaných měkkýšů.

Na každé ploše byly zapsány dva fytoecnologické snímky (van der Maarel 1979): větší o velikosti 75 x 75 cm a v jeho středu pak menší o velikosti 25 x 25 cm. Na menší ploše byla odebrána živá biomasa cévnatých rostlin pro stanovení vybraných chemických prvků (N, P, K, Ca), dále byly odebrány mechorosty a svrchní vzorek půdy pro výzkum měkkýšů (pouze u 9 transektů) a následně odebrán vzorek půdy z kořenové vrstvy rostlin pro stanovení prvků v půdě (Ca a organický C). Větší plocha sloužila k analýzám druhového složení a také jako rozšířená oblast pro výzkum měkkýšů (podrobnosti viz metodika článku II). Na každé ploše byla v nejsušším období roku (červenec až srpen) změřena vlhkost horní vrstvy půdy do hloubky cca 10 cm (ThetaProbe, sensor ML2x).



Obrázek 2. Schematické znázornění zápisu ploch na transektu.

Primární data všech fytoecnologických snímků včetně měřených faktorů jsou uložena v Národní fytoecnologické databázi České republiky (Chytrý & Rafajová 2003) pod čísly 113 592–113 627 (z publikace I) a 205 960–206 212 (z publikací II–IV).

Hlavní výsledky

Článek I

Ve dvou oblastech moravsko-slovenského pomezí (obr. 1) byla studována druhová bohatost cévnatých rostlin v prameništích vzhledem k jejich blízkému okolí. Počet druhů rostlin v prameništích koreloval s počtem druhů v okolní vegetaci jen v chladnější a vlhčí severovýchodní části zkoumaného území. V těchto prameništích byl nalezen vyšší podíl druhů okolní vegetace schopných růst ve slatinách. Naopak na lokalitách jihozápadní části území byl větší rozdíl mezi ekologickými podmínkami prameniště a okolí a jejich počty druhů nebyly vzájemně korelovány. Důležitým faktorem, který pravděpodobně omezoval pronikání druhů do pramenišť, byla vysoká specifita prostředí prameniště – srážení pěnovce a nedostatek živin, které omezují růst většiny rostlinných druhů.

Články II a III

Výrazné rozdíly v půdní vlhkosti (od 19 % v trávnicích do 97 % v prameništích) měly velký vliv na výměnu druhů všech tří skupin sledovaných organismů podél vlhkostního gradientu. Ačkoli změny druhového složení cévnatých rostlin, mechorostů i měkkýšů podél vlhkostního gradientu spolu navzájem korelovaly, ve změnách druhové bohatosti byl prokázán značný rozdíl. Počet druhů cévnatých rostlin vykazoval unimodální odpověď s optimumem posunutým do nižších hodnot vlhkosti. Druhová bohatost mechorostů lineárně klesala směrem k suchým trávnicím. Naopak žádná průkazná závislost vzhledem k vlhkostnímu gradientu nebyla potvrzena u měkkýšů, a to ani u počtu druhů ani u počtu jedinců. Procentuální zastoupení specialistů cévnatých rostlin i mechorostů rostlo se stoupající vlhkostí. Stejný trend byl pozorován i u podsouboru, který obsahoval pouze ohrožené a vzácné druhy cévnatých rostlin³.

Článek IV

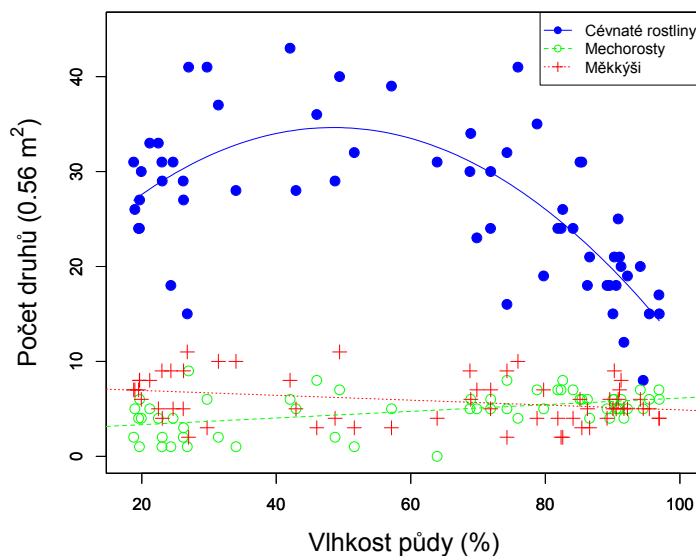
Některé vlastnosti cévnatých rostlin byly ve zkoumaném souboru dat preferovány, což potvrzuje teorii filtrování druhů stresujícím prostředím. Jedním z nich byla např. střední hmotnost semen, jejíž variabilita se mezi společenstvy prokazatelně měnila podél gradientu vlhkosti – hmotnost semen se zvyšovala směrem k sušším stanovištím. Celkově byly ve zkoumaných porostech druhy s lehkými semeny zastoupeny více než by odpovídalo náhodnému rozmístění druhů.

³ Za vzácné druhy jsou považovány taxony kategorií C1 až C4 z Červeného seznamu České republiky (Grulich 2012).

Diskuze a závěry

Výsledky této práce poukazují na výjimečnost prameništních společenstev ve vazbě na jejich okolní vegetaci. V první studii bylo prokázáno, že vliv okolí (tzv. *spatial mass effect*) nepůsobí na všech stanovištích stejně – jeho význam pro prameniště se lišil v závislosti na studované oblasti. Pokud byl velký rozdíl v ekologických podmínkách mezi prameništěm a okolím, vliv okolí se projevoval jen velmi slabě, což potvrzuje i práce Cantero et al. (1999) a teorie středních rozdílů (*Intermediate difference hypothesis*, Kunin 1998). Naopak v místech, která si byla podobnější (např. z hlediska vlhkosti půdy nebo přístupnosti živin), si byla ve své druhové skladbě podobnější i prameniště se svým okolím. Rovněž i z dalších studií této disertační práce vyplývá, že mnohé obecně přijímané zákonitosti neplatí u všech biotopů stejně (viz níže).

Výsledky předkládaných studií jasně prokazují vliv půdní vlhkosti (která nebyla jen odhadována, ale přímo měřena) jak na změnu druhového složení všech tří skupin studovaných organismů (cévnaté rostliny, mechorosty, měkkýši), tak i na některé vlastnosti cévnatých rostlin. Naopak vliv vlhkosti na počet druhů se mezi jednotlivými taxonomickými skupinami výrazně lišil a dokonce byly potvrzeny opačné výsledky než v dřívějších studiích. Narozdíl od předchozích výzkumů, kde počet druhů měkkýšů koreloval s půdní vlhkostí buď pozitivně (např. Wäreborn 1969, Martin & Sommer 2004 a, b) nebo unimodálně (Getz & Uetz 1994), výsledky naší práce ukazují spíše na slabě negativní (resp. žádnou signifikantně prokazatelnou) závislost. Opačný trend oproti dřívějším studiím byl popsán také u cévnatých rostlin. Ačkoli ve studiích jiných autorů koreloval počet druhů s vlhkosním gradientem většinou negativně (Dwire et al. 2004, Zelnik & Čarni 2008) nebo vůbec (Cachovanová et al. 2012), náš výzkum poukazuje spíše na unimodální závislost (podobně také Hou et al. 2008). Stejně výsledky jsou prezentovány i v obrázku 3, kde byly vybrány jen společné lokality pro cévnaté rostliny, mechorosty a měkkýše.



Obrázek 3. Vztah počtu druhů cévnatých rostlin, mechorostů a měkkýšů k měřené vlhkosti půdy.

Podobně se od některých dřívějších studií liší výsledky i dalších proměnných prostředí – druhová bohatost korelovala oproti očekávání (např. Hájková & Hájek 2003, Dwire et al. 2004, Hejman et al. 2010) s produktivitou pozitivně, což ale prokázali v případě bělokarpatských luk i Merunková et al. (2012). Hodnoty koncentrace vápníku v půdě byly na všech studovaných plochách poměrně vysoké (3 100–42 200 mg/kg), proto

pravděpodobně počet druhů mechorostů ani měkkýšů na tento gradient nereagoval. Také rozsah hodnot pH byl u studovaných ploch malý (6.0–8.0). Směrem k vápnatějším místům klesal významně pouze počet druhů cévnatých rostlin (narozdíl od prací Roem & Berendse 2000, Pärtel 2002, Cachovanová et al. 2012, Merunková & Chytrý 2012, Sekulová et al. 2012), což bylo způsobeno nejspíše provázaností tohoto gradientu s vlhkostí.

Tyto nesourodé výsledky jsou s největší pravděpodobností způsobeny specifickými podmínkami prostředí a vlastnostmi společenstev zkoumaných v této práci. Na relativně krátké vzdálenosti se vedle sebe vyskytují vlhká prameniště s pěnovcem a sušší trávníky, které patří k nejbohatším nelesním biotopům na světě (Klimeš 2008, Wilson et al. 2012). Naopak prameniště obsahují výrazně méně druhů cévnatých rostlin, především vlivem omezené přístupnosti živin. Ty jsou vázány ve vápnatých inkrustacích, a tudíž pro rostliny nepřístupné (Boyer & Wheeler 1989, Rozbrojová & Hájek 2008). Rozdílné výsledky (jak mezi třemi skupinami organismů navzájem, tak i mezi našimi a předchozími studiemi) mohly být zapříčiněny i dalším místním fenoménem, a sice flyšovými podložím, které je schopno absorbovat vodu a poté ji zpřístupnit v sušších obdobích roku (Škodová et al. 2011). To mohl být důvod, proč se některé druhy vlhkomilných organismů vyskytovaly i na sušších místech (z rostlin např. *Equisetum fluviatile*, *Eriophorum* spp., *Cratoneuron filicinum*, z měkkýšů pak např. *Vertigo angustior*).

Kromě vztahu k vlhkosti byly u tří studovaných skupin organismů prokázány vazby na některé další faktory prostředí. Počet druhů cévnatých rostlin i měkkýšů stoupal zároveň se zvyšující se hmotností biomasy, počet druhů mechorostů naopak spíše klesal. Mechorosty a cévnaté rostliny si na studovaných plochách konkurují (viz též např. u Nineemets & Kull 2005), kdežto pro měkkýše představuje více rostlinné biomasy a vyšší pokryvnost cévnatých rostlin větší heterogenitu prostředí. Ta je spojena s lepšími mikroklimatickými podmínkami a bohatší nabídkou potravních zdrojů (Cook 2001, Dvořáková & Horsák 2012). Naopak málo produktivní prameništní vegetace s převahou ostřic a suchopýrů poskytuje méně vhodných úkrytů a také omezenou skladbu potravy (Schamp et al. 2010). Po Bonferroniho korekci nekorelovala druhová bohatost mechorostů a měkkýšů s žádnými proměnnými prostředí (kromě korelace mechorostů s vlhkostí). Tyto dvě výše zmíněné skupiny jsou si podobné také např. z morfologického hlediska (velmi malá velikost těla, absence rozvinutých podzemních orgánů apod.)

Narozdíl od celkového počtu druhů daných skupin reagovaly na stejné gradienty prostředí podobně počty druhů specialistů cévnatých rostlin a mechorostů. Pozitivní vztah mezi poměrem specialistů cévnatých rostlin a vlhkostí odpovídal výsledkům práce Cachovanová et al. (2012). Také počet i poměr vzácných či ohrožených druhů cévnatých rostlin z Červeného seznamu České republiky (Grulich 2012) korespondoval s gradientem vlhkosti. Vzhledem k tomu, že prameniště sama o sobě představují vzácný biotop a vyskytuje se na nich jen omezené množství druhů, které z velké části patří mezi ohrožené, není tento závěr až tak překvapující, i když ke stejnému výsledku u trávníků došli i Merunková & Chytrý (2012). Analýza počtu vzácných druhů mechorostů nebyla v naší studii relevantní, jelikož ze 41 druhů bylo pouze osm s vyšším statutem vzácnosti než LC (*Least concern*, Kučera et al. 2012) a pouze tři z těchto druhů se vyskytovaly na více než pěti studovaných lokalitách.

Podle výsledků této disertační práce se zdá, že unimodální odpověď druhové bohatosti cévnatých rostlin na gradient vlhkosti nebyla přímo způsobena okrajovým efektem (který popisuje řada autorů – např. Łuczaj & Sadowska 1997, Orczewska & Glista 2005, Hou et al. 2008), ale čistě vlivem střední úrovně vlhkosti. Oproti předpokladu nebyly nejvyšší hodnoty počtu druhů ani ve středech transektů ani v sušších loukách, ale byly posunuty směrem do vlhčích luk. Ve stejném vlhkostrním rozmezí (37–60 %) bylo nalezeno i nejvíce druhů mechorostů, ačkoli jejich celkový trend byl vzhledem k vlhkosti pozitivně lineární. Tento výsledek podporuje domněnku řady prací (např. Klimeš 2008, Škodová et al. 2011,

Merunková et al. 2012), že vysoká druhová bohatost bělokarpatských luk je způsobena specifickou vlhkostí stanovišť, která umožňuje koexistenci suchomilných i vlhkomilných druhů rostlin.

Jak už bylo zmíněno v předchozím textu, vlhkost korelovala také s některými vlastnostmi rostlin. Například střední hmotnost semen v porostu byla ve zkoumaném souboru dat významně nižší, než by se dalo očekávat podle nulového modelu. Tento závěr koresponduje s prací v trávnicích Franzén (2004), ale neodpovídá výsledkům ze společenstev opuštěných polí (Schamp et. al 2008). Zároveň se hmotnost semen zvyšovala směrem k sušším stanovištím. Malá a lehká semena umožňují rostlinám lepší a rychlejší šíření i na větší vzdálenosti, což je výhodou vzhledem k izolovanosti a nízké početnosti pramenišť v krajině. Dále je možné, že malá semena snáze zaplní vhodné plošky v husté vegetaci a vytvoří zde více semenáčků, než by tomu bylo v případě větších semen.

Závěrem je možno konstatovat, že vlhkost půdy významně ovlivňuje rostlinná i živočišná společenstva a je vhodné ji věnovat pozornost i v dalších studiích.

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Is species richness of small spring fens influenced by the spatial mass effect?

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Abstract

Ecological theory predicts that the species composition of island habitats is, among others, shaped by the mass effect of nearby ill-adapted populations, but this has rarely been tested. We investigated small calcareous spring fens scattered within species-rich grasslands in a region in which particular locations differ in climatic and edaphic conditions. Fens in colder, moister and less calcareous north-eastern (NE) locations harboured more plant species from surrounding grasslands and displayed higher similarity with the surroundings than the fens in warmer, drier and more calcareous south-western (SW) locations. Fen species richness correlated significantly with surrounding species richness in the NE locations, whereas no correlation was found for the SW locations. Fens in SW locations are characterized by both intense tufa formation, which creates extreme ecological conditions, and the contrasting environmental conditions compared to surrounding grasslands. We demonstrated that the mass effect does not always significantly shape the species composition of island habitats and that the landscape species pool may not influence extreme habitats. This finding accords with the Intermediate difference hypothesis, which predicts a unimodal relationship between the strength of the spatial mass effect and the ecological similarity between neighbouring plots, and could be utilized in the selection of model habitats for exploring large-scale ecological phenomena without the possibly confounding spatial mass effects.

Key words: Carpathians, Coexistence, Grassland, Source-sink dynamics, Species pool, Vegetation, Vicinism

Abbreviations: NE – north-eastern; SW – south-western; RSP – regional species pool, LSP – local species pool, EIVs – Ellenberg indicator values; DCA – detrended correspondence analysis; PROTEST – PROcrustean Randomization TEST.

Introduction

It is generally accepted that the composition and species richness of a community is determined not only by local environmental conditions that filter adapted species from the species pool (e.g. Zobel 1997, Gough et al. 2000, Chytrý et al. 2007, Chiarucci et al. 2008), but also by the quality of surrounding habitats (e.g. Dunning et al. 1992, Skov 1997, Kunin 1998, Wisser & Buxton 2008). Nevertheless, the possible effect of the different species composition of surrounding habitats has more often been theoretically postulated and discussed rather than really tested in ecological studies (e.g. Stevens 2006).

It is often assumed that species may migrate among communities and that some of them may occur in a small island habitat only because of the strong influence of nearby source populations (Cottenie 2005, Ng et al. 2009, Zelený et al. 2010). This is called the *spatial mass effect* (sometimes also *ecological vicinism*, *source/sink dynamics* or *spillover effect* – Shmida & Wilson 1985, Dunning et al. 1992, Kunin 1998, for details on terminology see van der Maarel 1995 and Zonneveld 1995) and requires a continuous supply of propagules from the surrounding habitats. Without distinguishing between the species occurring due to the spatial mass effect and those that are well adapted, the set of species capable of co-existence in a habitat even for a short time is often considered as the habitat's species pool (e.g. Eriksson 1993, Sádlo et al. 2007).

The species pool concept has attracted much attention during the last two decades (e.g. Pärtel et al. 1996, 2001, Aarssen & Schamp 2002, Pither & Aarssen 2005, Hájek et al. 2007), and has resulted in the formulation of several interesting possible explanations of large-scale ecological and evolutionary phenomena. Species pool-oriented explanations, however, can be confounded by the spatial mass effect, which may cause ill-adapted species to occur in the habitat (Pither & Aarssen 2005, Hájek et al. 2007). Quantifying the strength of the spatial mass effect in different habitats and landscape contexts is therefore needed, but such studies are rare (e.g. Robson & Chester 1999, Zelený et al. 2010). More often, the effect of the surrounding matrix on species composition has been confirmed in the context of succession and vegetation recovery on disturbed or newly created habitats (Hatton & Carpenter 1986, Borgegård 1990, Ashworth et al. 2006, Řehouňková & Prach 2008). However, early successional stages are usually favourable for colonizing species and do not act as a sink for them in many cases; therefore these studies are not entirely relevant to testing the theory of the spatial mass effect (Kunin 1998). A more relevant study by Kunin (1998) found a slight but significant decline in species richness with distance from plot boundaries, i.e. a spatial mass effect, between neighbouring plots in a grassland experiment where habitat differences among the plots were great, but not extreme. He formulated the Intermediate difference hypothesis for the spatial mass effect, which predicts a unimodal relationship between the strength of the mass effect and the similarity between neighbouring plots: no mass effect at the “no-difference” level, a strong mass effect at the intermediate level and a weak mass effect in the case of extreme ecological differences between habitats. Nevertheless, Kunin's grassland data represented only the first half of the similarity gradient, i.e. rather small ecological differences between neighbouring habitats.

There are only a few studies comparing species lists between neighbouring, clearly delimited, more or less successional stable vegetation types (Cantero et al. 1999) or between isolated habitat islands and their surrounding matrix (Wisser & Buxton 2008). While the latter study conducted on volcanic rock outcrops found strong evidence of a spatial mass effect, Cantero et al. (1999) found that the number of species was positively dependent on contact communities only in the case of short-grass versus tall-grass prairie vegetation. In the former, low competition for light enabled co-existence of more plant species. Moist depressions were not affected by the spatial mass effect. The results of Cantero et al. (1999) thus suggest that the strength of the spatial mass effect may vary

among different habitats and plant communities. In the light of the Intermediate difference hypothesis we would expect generalists from the surrounding matrix to be relatively less successful in germinating and establishing in extreme island habitats compared to less extreme ones. Extreme habitats will therefore be less influenced by the spatial mass effect. We found a suitable study system to test this prediction: a system of small, isolated calcareous spring fens scattered within a mosaic of managed species-rich grasslands in the West Carpathian flysch zone (Hájek et al. 2002, 2007, Hájková et al. 2008). In comparison to the extremely species-rich surrounding plant communities, spring fens do not contain as many plant species because of the extreme ecological conditions and prevalence of specialists (Hájková & Hájek 2003). The high level of base saturation is the main factor determining the vascular plant species richness and composition of these fens (Hájek et al. 2002, 2007, Hájková & Hájek 2003). In addition, the vegetation of the most calcium-rich tufa-forming fens is limited by phosphorus deficiency (Rozbrojová & Hájek 2008). However, some spring fens contain more grassland generalists regardless of their water chemistry and nutrient availability (Hájková & Hájek 2003, Hájek & Hekera 2004).

The aim of this study was to utilize the abovementioned habitat islands to explore the role of the spatial mass effect in shaping their species richness and composition and to test the prediction that the mass effect does not always occur in the same habitat depending on a landscape context. We predict that a great environmental dissimilarity between tufa-forming fens and surrounding grasslands in the warmer, drier and more calcareous SW region will lead to (i) greater floristic dissimilarity between spring fens and surrounding, (ii) less realisation of local species pool of grassland species capable to grow in fens, (iii) no correlation between species richness in fens and in its surrounding. For NE locations we predict the opposite pattern.

Material and methods

Study area

The study area is situated on the border between the Czech and Slovak Republics in Central Europe (Fig. 1). The area belongs to the West-Carpathian flysch zone, where the bedrock is composed of alternating claystones and sandstones. These rocks are variable in their chemistry. Calcium-rich layers supporting tufa (travertine) precipitation occur most often in the south-west and less often in the north-east. The small islands of spring wetlands under study cover 0.02–0.2 ha, of which well-developed sedge-moss calcareous-fen vegetation usually cover mostly only a few square metres around spring outflows. The surrounding grasslands cover much larger areas (up to hundreds of hectares in extreme cases). There is a distinct climatic gradient running from south-west to north-east: the annual mean precipitation increases from 625 mm in the south-west to 1400 mm in the north-east. The annual mean temperature is between 7.5 °C (south-west) and 3 °C (north-east) (Miklós 2002, Tolasz 2007). The fens are situated on the slight slopes between 330 and 730 m a.s.l.

Of those fens in the study area (according to Hájek & Horsák 2005) we selected all calcareous and extremely-rich fens (i.e. fens without *Sphagnum* occurrence classified within the *Caricion davallianae* alliance in the phytosociological system, cf. Hájek et al. 2006) that were surrounded by managed (mowed or grazed) grassland vegetation of a minimum area of 0.8 hectares. Thus, 36 spring fens were selected in total. The surrounding grassland vegetation was mostly comprised of wet herb-rich grassland and moist to semi-dry grasslands (classes *Molinio-Arrhenatheretea*, *Calluno-Ulicetea* and *Festuco-Brometea*; according to Chytrý 2007).

According to geographical position and climatic conditions we divided localities into two groups: the north-eastern (generally colder and moister) group which contained 20 localities and the south-western (generally warmer and drier) group with 16 localities.

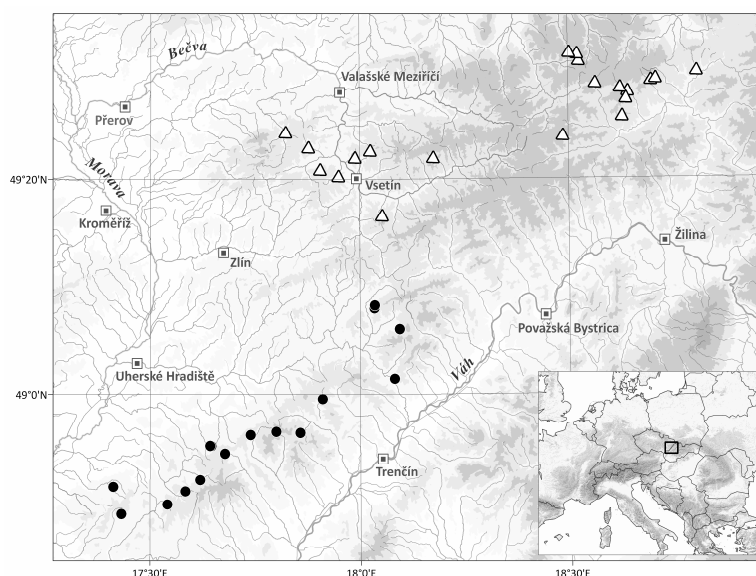


Figure 1. Location of the studied spring fens. Triangles refer to colder, moister and less calcareous NE locations, whereas circles refer to warmer, drier and more calcareous SW locations.

Data collection

A total of 36 vegetation plots in spring fens and 36 species lists from their surrounding non-forest vegetation were recorded during June and July 2003 and 2004. The surroundings were defined as a 50 meters wide circle, along the fen edge, beginning one meter from the border of the fen relevé. All vascular plants were identified in the vegetation plots of 16 m² placed in the wettest part of each fen. Spring fen vegetation (*Caricion davallianae*) was mostly distributed as small isolated islands in the study area and the standard sample plots of 16 m² usually covered a large fraction of their extent.

Species nomenclature generally follows Kubát et al. (2002), though a broader taxonomical concept was sometimes applied due to difficulties in identification of sterile plants or juveniles to the species level.

According to the methodology and terminology of the species pool concept (e.g. Pärtel et al. 1996, Zobel 1997, Zobel et al. 1998, Dupré 2000, Sádlo et al. 2007) we determined the *regional species pool* (RSP) of spring fens, separately for both SW and NE areas, as a set of species that can occur in the habitat, i.e. as the species with at least one occurrence in any spring fen in the study area. These data were taken from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) and own data from Slovakia. The data set contained 180 relevés from NE region and 177 relevés from SW region. Consequently we determined the *local species pool* (LSP) of each fen as a set of species from the regional species pool that was actually found in the surrounding of the fen. From all statistical analyses we deleted 12 narrow-niche fen specialists – the species that are closely linked to spring fens in the study area (*Blysmus compressus*, *Carex davalliana*, *C. flava* agg., *Eleocharis quinqueflora*, *Epipactis palustris*, *Eriophorum angustifolium*, *E. latifolium*, *Menyanthes trifoliata*, *Parnassia palustris*, *Polygala amarella*, *Triglochin palustre* and *Valeriana simplicifolia*). This step was done because our aim was to test the mass effect of surrounding habitats to fens, but not *vice versa*. The definition of particular species lists is summarised in Fig. 2.

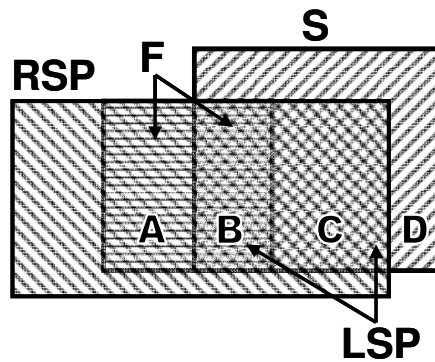


Figure 2. The definition of particular species lists used in the analyses. For each locality we obtained the complete list of species found in the fen (F) and the complete list of the species found in the surrounding of the fen (S). According to the database of fen relevés from the entire study area (separately for SW and NE) we further defined regional species pool (RSP) of fens. For each locality, the species found in fens were classified into the species group found only in fen and not in the surrounding (species group A, not considered as a result of the fen-surroundings interaction) and the species group of the RSP found in both the fen and the surroundings (species group B, realised local species pool). The species found only in the surrounding and not in the fen were classified into the species group belonging to

fen RSP (species group C, the species capable to grow in fen, but not growing in the fen in the target locality, i.e., the non-realised local species pool) and the species group that never grow in fens (species group D). The species groups B and C together create the local species pool (LSP), which was for each locality defined as an intersection of RSP and the species actually found in the surroundings.

Data analysis

For the description of the pattern of environmental conditions in fens and their surroundings in the SW and NE locations, we used Ellenberg indicator values (EIVs; Ellenberg et al. 1992). EIVs are empirically established classes of Central-European vascular plant species with a similar ecological niche along the target gradient. Values are given on a 9-point scale (1 is lowest, 9 is highest) for light, temperature, soil reaction and nutrients and on a 12-point scale for moisture (1 is driest, 12 is wettest). All these values were calculated for both species lists (fen, surroundings) at each locality using JUICE 7.0.58 software (Tichý 2002). The 12 fen specialists (see above) were not deleted from fens in this computation.

Results of detrended correspondence analysis (DCA) of the species lists of the two groups of fens and surroundings were compared using PROTEST (PROcrustean Randomization TEST; Jackson 1995). As a reference matrix we used the scores of the first four DCA axes of fens, while the first four DCA axes scores of surroundings were used for the rotation matrix. 9999 random permutations were used in each test.

The site scores on the first DCA axis of the species list of the surroundings were further used as the expression of the environmental gradient running between SW and NE locations, and it is hereinafter referred to as the “SW-NE environmental gradient” (Fig. 3).

The Jaccard dissimilarity of species list pairs from each locality was calculated. Non-parametric Spearman correlation in Statistica 9.1 software (StatSoft, Inc. 2010) was used for the testing of the relationship between the SW-NE environmental gradient and the Jaccard dissimilarity, the relationship between the species richness of spring fens (without 12 narrow-niche fen specialists, see above) and the size of the local species pool, as well as the relationship between the proportion of the local species pool found in a fen (12 fen specialists not considered) and the SW-NE environmental gradient.

Results

Pattern description

Spring fens are significantly moister, colder and lighter than their surroundings in all locations, and poorer in nutrients than the surrounding grasslands in NE locations (Fig. 4). On the other hand, base saturation (soil reaction) obviously reflects local geological bedrock and do not differ substantially between the fens and the surrounding grasslands. Both the fens and the surrounding grasslands contained more species from base-rich habitats in SW than in NE locations. The SW-NE environmental gradient coincided especially with the

Ellenberg's temperature, moisture and soil reaction. As was initially expected, the surrounding grasslands seem to be drier, warmer, nutrient-poorer and more alkaline (i.e. more calcareous) in SW than in NE locations (Fig. 3, 4).

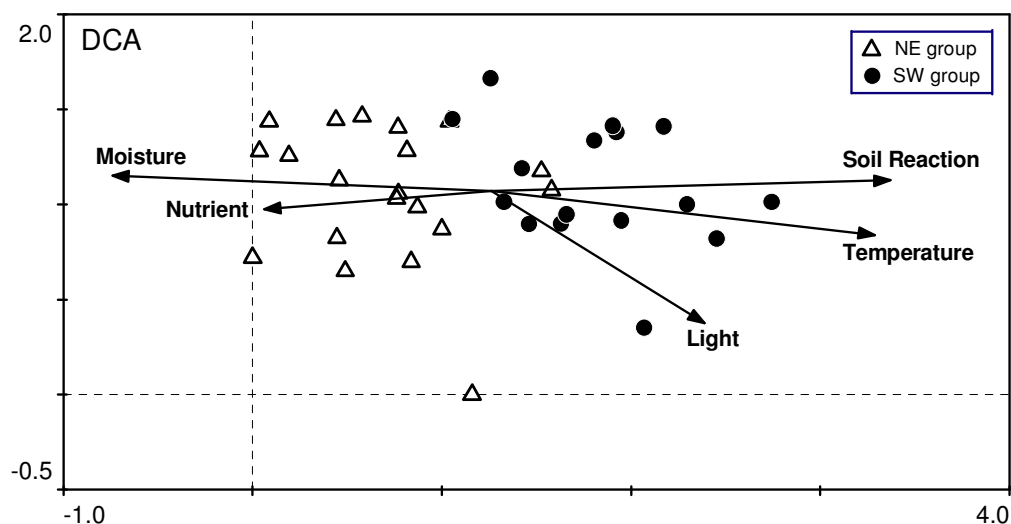


Figure 3. Detrended correspondence analysis of the species lists of the fen surrounding, with EIVs plotted as supplementary environmental data. The first axis shows the gradient between colder, moister and less alkaline (calcareous) NE locations and warmer, drier and calcareous SW locations. The site scores on the first DCA axis express the SW-NE environmental gradient. Percentage variance explained by first ordination axis was 10.9%, eigenvalue = 0.365.

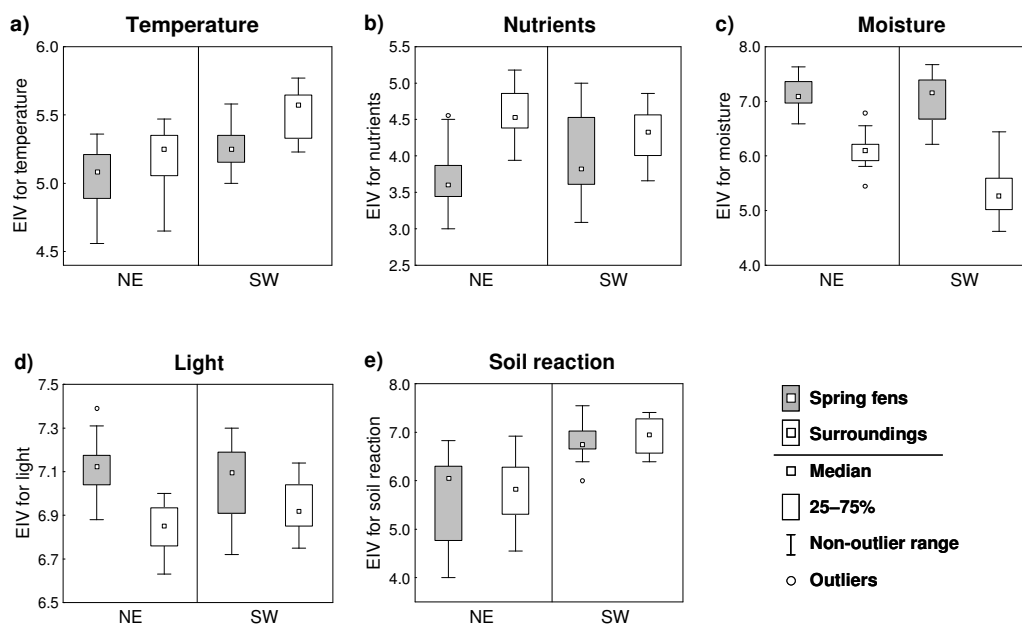


Figure 4. Pattern in differences in ecological conditions between spring fens and their surroundings in NE and SW locations, as indicated by mean Ellenberg indicator values (a-e) for all vascular plants present in the species lists.

Species richness

The numbers of species richness in fens and surroundings on particular study localities are shown in Table 1. The most species-rich fen contained 55 species, whereas the poorest one had 18 species. The species-richest surrounding harboured 152 species.

Statistical testing

The Jaccard dissimilarity correlated significantly ($r_s = 0.525$, $p < 0.05$) with the SW-NE environmental gradient. The species compositions of the fen and its local species pool were more similar in the NE than in the SW locations.

The species richness of spring fens (without 12 fen specialists) did not correlate significantly with the size of the local species pool ($r_s = 0.188$, $p > 0.05$). When data subsets were analyzed separately, the Spearman correlation between the species richness of spring fens and of the local species pool was significant for the NE locations ($r_s = 0.589$, $p < 0.05$, Fig. 5a), whereas no correlation ($r_s = -0.444$, $p > 0.05$) was found for the SW locations (Fig. 5b).

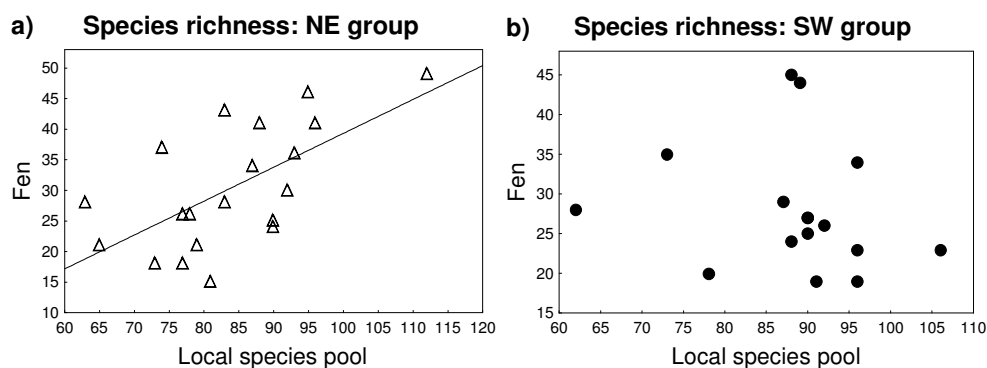


Figure 5. The relationship between the fen species richness and the size of the local species pool in NE (a) and SW (b) locations. The narrow-niche fen specialists ($n = 12$) are not considered in species counts.

There were more species from the local species pool that actually appeared in spring fens in NE than in SW locations (Fig. 6); the Spearman correlation between the proportion of local species pool found in fens (without 12 fen specialists) and the SW-NE environmental gradient was statistically significant ($r_s = -0.438$, $p < 0.05$).

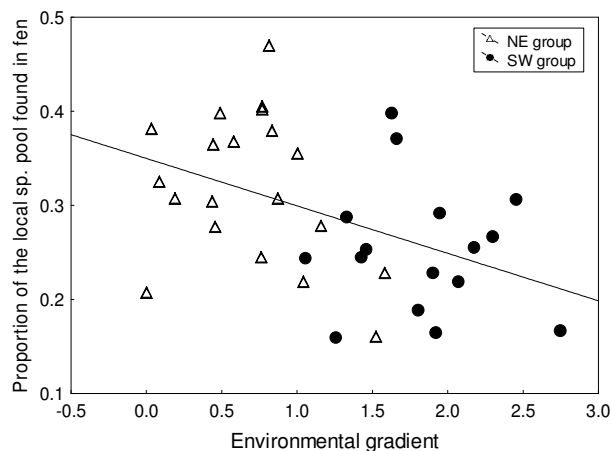


Figure 6. The proportion of the local species pool found in spring fens, i.e. $B/(B+C)$ in Fig. 2 and K in Table 1, plotted against the SW-NE environmental gradient (site score on the first DCA axis for the surroundings). 12 narrow-niche fen specialists were not considered.

Comparison of fens and surroundings using Procrustean analysis was highly significant for the NE locations ($m^2 = 0.5679$; $p = 0.0002$; 9999 permutations), whereas the significance for the SW locations was weaker ($m^2 = 0.6325$; $p = 0.0063$; 9999 permutations). This result shows that species composition of fens and their surrounding are more similar in their gradient structure in the NE locations than in the SW locations and accords therefore with the other results.

Table 1. Number of species in fens and their surroundings on particular study localities. Letters A–D refer to the groups described in the Fig. 2; letters E–K refer to their combinations.

Relevé nr.	Group	A	B	C	D	E	F	G	H	I	J	K
		Species found only in fen	Realised sp. pool	Non realised sp. pool	Species found only in surroundings	Sum of all species on locality	A+B	F-G	B+C+D	B+C	B/J	
1	SW	13	35	53	13	114	48	3	45	101	88	0.4
2	SW	16	21	52	4	93	37	2	35	77	73	0.29
3	SW	10	22	65	6	103	32	3	29	93	87	0.25
11	SW	7	16	80	56	159	23	4	19	152	96	0.17
19	SW	13	14	74	9	110	27	3	24	97	88	0.16
20	SW	14	33	56	13	116	47	3	44	102	89	0.37
21	SW	5	19	59	3	86	24	4	20	81	78	0.24
22	SW	5	22	68	8	103	27	2	25	98	90	0.24
23	SW	9	28	68	15	120	37	3	34	111	96	0.29
24	SW	7	15	76	19	117	22	3	19	110	91	0.16
25	SW	7	21	71	24	123	28	2	26	116	92	0.23
26	SW	7	20	86	13	126	27	4	23	119	106	0.19
32	SW	6	21	75	39	141	27	4	23	135	96	0.22
33	SW	9	23	67	28	127	32	5	27	118	90	0.26
34	SW	6	24	66	35	131	30	3	27	125	90	0.27
36	SW	12	19	43	27	101	31	3	28	89	62	0.31
4	NE	5	13	68	9	95	18	3	15	90	81	0.16
5	NE	8	18	61	13	100	26	5	21	92	79	0.23
6	NE	4	16	57	9	86	20	2	18	82	73	0.22
7	NE	9	39	44	13	105	48	5	43	96	83	0.47
8	NE	3	25	65	17	110	28	3	25	107	90	0.28
9	NE	10	33	60	12	115	43	7	36	105	93	0.35
10	NE	2	20	45	4	71	22	1	21	69	65	0.31
12	NE	3	16	61	12	92	19	1	18	89	77	0.21
13	NE	8	23	60	15	106	31	3	28	98	83	0.28
14	NE	10	45	67	23	145	55	6	49	135	112	0.4
15	NE	4	28	64	12	108	32	2	30	104	92	0.3
16	NE	5	24	39	2	70	29	1	28	65	63	0.38
17	NE	4	24	54	9	91	28	2	26	87	78	0.31
18	NE	3	25	52	9	89	28	2	26	86	77	0.32
27	NE	9	35	61	17	122	44	3	41	113	96	0.36
28	NE	8	35	53	22	118	43	2	41	110	88	0.4
29	NE	10	30	44	6	90	40	3	37	80	74	0.41
30	NE	13	36	59	7	115	49	3	46	102	95	0.38
31	NE	6	32	55	12	105	38	4	34	99	87	0.37
35	NE	11	22	68	4	105	33	9	24	94	90	0.24

Discussion

The results support our initial hypothesis about the different contributions of the spatial mass effect to the actual species composition and richness of a similar habitat in a different landscape context: the species richness of mostly peat-forming fens in colder, moister and less calcareous NE locations was more apparently influenced by the landscape matrix than that of the mostly tufa-forming fens in the warmer, drier and more calcareous SW locations. In the SW region (the Bílé Karpaty Mts), the extreme species richness of intermittently wet to semi-dry grasslands (the *Molinion caeruleae* and *Bromion erecti* alliance), which is extraordinarily high at the European scale (Klimeš 2008), had absolutely no relationship with the species richness of the scattered spring fens; their species richness was, in contrast, rather low (see also Hájková & Hájek 2003). Our result from SW locations thus corresponds with that of Dauber et al. (2003) who found a rather small spatial mass effect on habitats' species richness as compared to the effect of habitat patchiness. Nevertheless, our results from NE locations support the spatial mass effect on the species composition of habitat islands as in the study of Wisser & Buxton (2008) or in the case of short-grass vegetation in the study of Cantero et al. (1999).

The possible interpretation of the discrepancy between the results from NE and SW locations can be related to the different level of ecological similarity between fens and their surroundings in these two landscapes. The contrast in moisture conditions between fens and surrounding grasslands in the SW locations is the most likely explanation of the fact that a large number of species occurring in semi-dry grasslands is not able to establish in waterlogged spring fens at all. This simple explanation matches Kunin's intermediate difference hypothesis (Kunin 1998), which predicts a slight or no mass effect when the habitat difference is great. Although Kunin assumed no mass effect especially for neighbouring habitats that have no shared species pool, we observed that the proportion of the local species pool found in a fen significantly decreased towards warmer, drier and more calcareous SW locations. This suggests that local factors somehow filter species from the local species pool in calcareous fens in the warmer SW locations. We interpret this result based on the knowledge of phosphorus deficiency in fens with tufa formation (Boyer & Wheeler 1989). The intensity of tufa formation increases towards SW locations in our study area (Hájek et al. 2002). The evidence of decreasing phosphorus availability with increasing amount of calcareous tufa in our study area was obtained especially from the significantly higher N:P biomass ratio in tufa-forming fens (Rozbrojová & Hájek 2008). Mean water phosphate concentration was, by analogy, two times higher in peat-forming than tufa-forming fens in the study of Hájek et al. (2002), which used single-sample water chemistry data. However, this difference was not statistically significant, perhaps because of considerable fluctuation of phosphate concentration during a year (Hájek & Hekera 2004). The low P-availability in tufa-forming fens may explain why nutrient-requiring grassland species from extremely species-rich surrounding grasslands (e.g. *Lotus corniculatus*, *Anthoxanthum odoratum*, *Prunella vulgaris*, *Leontodon hispidus*, *Rumex acetosa*, *Plantago lanceolata*, *Vicia craca*, *Ajuga reptans*, *Luzula campestris* or *Trifolium repens*) are very rare in tufa-forming spring fens, although they can establish more frequently in peat-forming fens in NE locations. Some of these species also appeared to be responsible for the spatial mass effect in the Kunin's study (1998).

Our results are thus in agreement with the results of Cantero et al. (1999) and Kunin (1998), and support the idea that the intensity of the spatial mass effect is context-sensitive. Cantero et al. (1999) questioned whether species richness depends on the quality of the surrounding stands, and demonstrated that the spatial mass effect was an important determinant of species composition and richness only in one vegetation type out of three (short-grass vegetation). They believed this was due to the lower competition for light in less productive habitats. Our results do not support this explanation since fens in SW and

NE locations either do not differ in productivity or fens in NE locations are even more productive due to better nutrient availability (Hájková & Hájek 2003, Rozbrojová & Hájek 2008). We could therefore answer Cantero's initial question in such a way that species richness (and composition) is more dependent on the surrounding stand when this stand is more similar regarding habitat conditions, or when the study habitat is less extreme with respect to nutrient availability or other factors that may prevent the occurrence of generalists. However, further research is needed to verify this hypothesis.

One may argue against our conclusion that the successional status of the vegetation type is another factor influencing the similarity between a vegetation type and its surroundings. Borgegård (1990) found that well-established communities of old gravel pits were more similar to the surrounding vegetation than young, successional unstable communities. This result, however, cannot be extrapolated to our study fens, which all represent the same successional stage and whose Holocene history is very similar (Rybníčková et al. 2005; see also exact age data for the Outer Carpathian region in Hájek et al. 2011).

We have provided the support for the Intermediate difference hypothesis for the spatial mass effect at the community level. We further have demonstrated that the surrounding landscape matrix does not always influence the species composition of island habitats and that the local species pool does not have to influence the species composition of extreme habitats. This finding, together with the results of Cantero et al. (1999) or Robson & Chester (1999), illustrates the need for more studies on the spatial mass effect in different habitats. In the light of their evidence of the matrix effect on the species composition of island habitats, Wisser & Buxton (2008) have called into question an application of metapopulation and island-biogeography theories to island-like inland habitats. Our results suggest that such a call may be premature.

Our study is the first to demonstrate explicitly the weakening of the mass effect when environmental contrast between fens and their surrounding increases and adds to the evidence for the Intermediate difference hypothesis in this way. The conclusion that a greater difference in ecological conditions between habitats means a less pronounced mass effect may sound trivial, but we consider it an important piece of knowledge that may be utilized in the selection of appropriate study habitats for testing the hypotheses regarding island biogeography, metapopulations, species pool or evolutionarily driven species-richness-environmental relationships. Here, the spatial mass effect may obscure the effects of island-habitat properties. Fens and springs, for example, have often been studied in humid boreal, arctic or alpine zones, where their species richness, composition and the ratio between generalists and specialists is influenced more by the surrounding stands than in the regions where fens and springs are ecologically more sharply delimited against the surroundings. By analogy, phosphorus-limited calcareous fen vegetation composed mostly of specialists would be a more appropriate model habitat for testing some biogeographical hypotheses or vegetation-environment relationships than circumneutral fens with better nutrient availability that may harbour many species from the surrounding grasslands (e.g. Hájek et al. 2006, 2008, Rozbrojová & Hájek 2008).

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Patterns of land snail assemblages along a fine-scale moisture gradient

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Abstract

We studied changes of terrestrial snail assemblages over a gradient of soil moisture using 60 sampling plots in the White Carpathian Mountains of the south-eastern Czech Republic. We used within-site design to control for confounding effects of site characteristics other than humidity, and we directly measured soil moisture along nine transects at distinct locations. Each transect had from 4 to 16 plots, and it was laid down from wet calcium-rich spring fen habitats to semi-dry meadows in the fen surroundings. We observed a sharp moisture gradient along each transect, with the measured soil moisture varying from 97% in fen plots to 19% in semi-dry grassland plots. Altogether 29 land snail species and 4 213 live individuals were collected. Species richness of land snails varied from 2 to 11 species per plot. However, we did not observe any significant linear or unimodal response of species richness or total abundances to measured soil moisture. In contrast, sharp compositional changes along studied transects were found, suggesting differences in species preference to soil moisture conditions at fine, within-site scale. Among 21 species with the frequency higher than five, 10 (after a Bonferroni correction) showed a significant response to soil moisture. Three species expressed significant affinity to drier plots, five species were more abundant in moister plots and only two species preferred middle values. In several previous studies, both linear and hump-shaped relation between soil moisture and number of land snail species were documented. This raised questions about general response of land snails to soil moisture and the importance of possible bias caused either by using only estimated values of site moisture or sampling in distinct sites differing also in other environmental factors that might potentially overtopped importance of soil moisture for land snail distribution.

Key words: calcareous fens, grasslands, molluscs, soil moisture, species optima, species richness, vegetation

Introduction

Many previous studies on land snail community ecology have shown a positive response of species richness and mostly also total abundances to content of available calcium and/or soil pH (e.g. Wäreborn 1969; Horsák 2006). This pattern seems to operate at both larger (regional) and smaller (within-site) scales (Juříčková et al. 2008). The amount of calcium also dictates changes in species composition, with the majority of species having their optima at calcium-rich sites (Hylander et al. 2005; Horsák et al. 2007), but Nekola (2010) found many strictly acidophilus species in a North American fauna. Soil moisture is the second most frequently, but notably less often than calcium, reported environmental predictor of land snail distribution (e.g. Martin & Sommer 2004a, b), because snails are sensitive to desiccation (Cook 2001). However, contrary to calcium content and soil pH, soil moisture has rarely been directly measured (but see Wäreborn 1969). It was mostly only estimated (Getz & Uetz 1994; Chiba 2007) or studied sites were classified into several moisture categories (Martin & Sommer 2004a, b). Some studies used Ellenberg indicator values (Ellenberg et al. 1992) as a proxy for soil moisture obtained from vegetation samples (Čejka et al. 2008; Čejka & Hamerlík 2009). These estimates were found to perform well in land snail ecology studies (Horsák et al. 2007).

However, all previous studies assessing the influence of soil moisture on land snail distribution have analysed assemblages of isolated and distant sites, mostly at relatively large, regional sampling scale. This sampling protocol may introduce bias, caused by other site characteristics independent of soil moisture, which can influence land snail distribution as well.

Confounding effects of soil moisture and calcium content were already documented in several studies. Wäreborn (1969) found a positive effect of soil moisture only at dry meadow wood series, but no effect of calcium. In wet meadow wood series, however, the amount of calcium was closely related with the snail species richness. Martin & Sommer (2004b) found no effect of soil pH in dry forest sites, but a positive response was observed at damper forest habitats.

In this study, we attempt to avoid the drawbacks of previous studies and to analyse land snail assemblage patterns along a steep soil-moisture gradient along a transect from a treeless calcareous-fen community to a dry calcium-rich meadow. To obtain more general results, we settled transects at nine distinct locations, but within a climatically and geologically uniform area. Our aims were to study response of snail species richness, total abundance and composition along a fine-scale gradient of soil moisture. We also analysed the pattern of species composition changes along the gradient – species turnover or their accumulation toward plots of certain soil moisture values (i.e., higher, middle or lower) – using species response curves. On the basis of above-referred published data, it is difficult to predict whether soil moisture controls both species richness and species composition or only one of them. If there is a significant effect on the species richness, we can predict two possible responses that have been reported in the literature – a linear decrease towards drier sites (Wäreborn 1969; Martin & Sommer 2004a, b) or a hump-shaped response, with a peak at intermediate moisture values (Getz & Uetz 1994; Chiba 2007).

Methods

Study area

The study area is situated in the southern part of the border between the Czech and Slovak republics in the White Carpathian Mountains and adjacent southern part of the Vsetínské Mountains, a part of the western Carpathians. This area is formed by flysh, the bedrock composed of alternating clay stones and sandstones (Poprawa & Nemčok 1988).

Annual mean precipitation is approximately 700 mm and annual mean temperature is about 7.5 °C (Miklós 2002; Tolasz 2007). Localities were situated between 270 and 550 m a.s.l. Vegetation consisted of both meadow calcareous tufa-forming spring fens classified as the *Caricion davallianae* alliance (cf. Hájek et al. 2006) and of semi-dry grasslands classified as *Festuco-Brometea* class (alliance *Cirsio-Brachypodium pinnati* or *Bromion erecti*). There were also ecotonal communities, classified within *Calthion* alliance, located between these two vegetation types in some locations. Nomenclature of vegetation follows Chytrý (2007). The geological structure, climatic conditions and vegetation of the study area are in detail described by Horsák (2006) and Jongepierová (2008). Studied sites were *a priori* chosen to represent as long as possible within-site gradient of soil moisture and vegetation structure (Schamp et al. 2011). We investigated places where both moist spring fen and dry grasslands occurred alongside. Snail fauna of treeless spring fens was found to belong to the most species-rich snail assemblages of the region (Dvořáková et al. 2011), holding the highest number of species among grassland habitats (Horsák 2008).

Field sampling and environmental variables

Data were collected in June and July during the years 2005–2008. At each of nine study locations, one linear transect (7–31 meters) was laid out from the moistest part of spring fen to the dry grassland surrounding the fen. The number of plots varied from 4 to 16 per transect, depending on the size of spring fen. The size of each plot was 75 cm x 75 cm and the distance between centres of two neighbouring plots was two meters. In total, 60 plots were sampled.

To sample mollusc assemblages, a central nested sub-plot (25 cm x 25 cm) of each plot was cut just below ground level, using a sharp knife, and removed along with the herbaceous vegetation, mosses, litter and the upper soil layer. To obtain more precise information about the entire assemblages of the plot, we also randomly collected 3 litres of the upper layer from the remaining part of sampled plot. Plots were not cut completely to reduce negative impact of the sampling on fen communities. Samples from fen habitat were processed using the “wet sieving method” (Horsák 2003) and then air dried. Samples from grasslands were dried immediately after the sampling. After drying, shells were separated from the remaining material by hand sorting under a stereo microscope, identified and counted, separating live individuals and empty shells. We analysed only live individuals, because the calcium rich environment of study sites supports shell accumulation over a relatively long time period (Cernohorsky et al. 2010). This can introduce a significant bias in the data, as empty shells of species inhabiting adjacent habitats can frequently be found. Because the sampling was designed to extract snail individuals from sampling volume, live individuals show an exact snail assemblage of the plots; we did not record any important seasonal variation in species' occurrences at fens in the study region (M. Horsák, unpubl. data). We also carried out all analyses based on all recorded shells (live individuals and empty shells together), and we obtained basically the same results as presented below (data not shown). This suggests that the observed patterns are stable over the season. Mollusc nomenclature follows Horsák et al. (2010), with authorities given in Table 1. Slugs were not included in this study, as the sampling method used was not suitable to determine slug abundance (cf. Oggier et al. 1998). Moreover, there is only one species, *Deroceras laeve* (O. F. Müller 1774), which occupies spring fens more frequently; occurrence of further slug species is mostly accidental.

Moisture in the upper layer of the soil horizon was measured on each plot during dry period of the year (July to September) using a moisture meter (ThetaProbe, soil moisture sensor ML2x). To gather more information about environmental conditions in each plot, cover of vascular plants, mosses, and all plants together were estimated. Samples of vascular

plant standing biomass and upper soil layer were taken from each nested sub-plot just before the sampling of mollusc assemblages. Concentration of nitrogen and calcium were subsequently analyzed from dried and weighed plant biomass; volume of calcium was determined also from soil samples. Before chemical analyses, the plant biomass samples were air-dried at 70 °C. For nitrogen determination, dry material was mineralised with sulphuric acid and hydrogen peroxide, and the nitrogen concentration determined by the distilling method using a Kjeltac apparatus. For determination of calcium, material was mineralised in a sealed system, using microwave heating. Calcium concentration was determined by atomic absorption spectrophotometry (Zbiral 1994). Plant-available calcium in the soil was extracted using the Mehlich III method (strong acid extraction with ion complex) and determined by atomic absorption spectrophotometry (Zbiral 1995). Soil pH was not used in the analyses, because a range of values was too narrow (pH_{H2O} 6.2–8.0), as base-rich soils occurred at all plots, and no pH effect was found in preliminary analyses (data not shown).

Data analysis

Altogether 29 land snail species, 353 of their records and 4 213 live individuals were collected. For comparison of species richness between plots, two variables were introduced: (1) species richness, represented by a count of all species in a target plot and (2) proportional representation of snail species, calculated by dividing number of species found in a target plot by all species found in the target locality. Relationships between variables representing species richness and number of individuals on one hand and all measured variables on the other were statistically explored by Spearman's rank correlation coefficient in STATISTICA 10 program (Statsoft, Inc. 2011). A Bonferroni correction was used to remove the problem with multiple testing.

To find the main ecological gradients in snail species data, we used detrended correspondence analysis (DCA; Hill & Gauch 1980) in CANOCO 4.5 program (ter Braak & Šmilauer 2002). Species abundance of snails were log-transformed as $Y = \log_{10}(n+1)$ before the ordination analyses to reduce the influence of dominant species and to extract the pattern based mainly on presence/absence data, as some changes in population sizes can occur during the season. The environmental variables with significant relationship with ordination axes for snail species composition were determined using Spearman's rank correlation coefficient. Relationship between number of species and plot scores on the first DCA axis was explored by the Generalised Linear Models (GLM; McCullagh & Nelder 1989), with Poisson distribution function, calculated in R program (version 2.12.2; R Core Team 2012). Significances of linear and quadratic response were compared by Chi-square test.

Snail species response curves were modelled for species with more than five occurrences in the dataset. Non-transformed species abundance (density) was used to explain the distribution of species along the moisture gradient. We applied Generalised Additive Models (GAM; Hastie & Tibshirani 1990) with Poisson distribution, as implemented in CanoDraw for Windows 4.0 program (ter Braak & Šmilauer 2002). Selection of the best fitted regression model was done manually based on Akaike information criterion (AIC; Akaike 1974), and its significance was tested using F-test. Three categories of response curve shapes were subjectively distinguished: (1) an increasing monotonic response towards the dry part of moisture gradient or (2) towards the wet part, and (3) a unimodal response curve with optimum in the central part of the gradient.

Table 1. List of all land snail species recorded based on live individuals in all study plots. Frequency (Freq.) is a number of plots with the species occurrence, density (Dens.) is total number of live individuals recorded. Results of species abundance response curve modelling (GAM) for soil moisture (Opt.; species optimum in dry plots = D, wet plots = W, in the middle of the moisture gradient = M) and the model significance (P) are given, x = no candidate additive model had AIC value lower than the null model. Significant correlations after Bonferroni correction are in bold ($P < 0.00238$).

Abbrev.	Species name	Freq.	Dens.	F	P	Opt.
PunPyg	<i>Punctum pygmaeum</i> (Draparnaud, 1801)	39	651	x	x	-
CocLub	<i>Cochlicopa lubrica</i> (O. F. Müller, 1774)	38	598	2.84	0.05	-
VerPyg	<i>Vertigo pygmaea</i> (Draparnaud, 1801)	37	544	47.9	< 0.001	W
TruCyl	<i>Truncatellina cylindrica</i> (A. Férussac, 1807)	21	1026	11.15	0.001	D
VerAng	<i>Vertigo angustior</i> Jeffreys, 1830	21	174	2.24	0.094	-
PerHam	<i>Perpolita hammonis</i> (Ström, 1765)	20	138	5.67	0.02	D
VerAnt	<i>Vertigo antiovertigo</i> (Draparnaud, 1801)	20	185	19.55	< 0.001	W
VitPel	<i>Vitriina pellucida</i> (O. F. Müller, 1774)	17	202	46.2	< 0.001	D
CarMin	<i>Carychium minimum</i> O. F. Müller, 1774	14	75	3.62	0.019	M
PliLub	<i>Plicuteria lubomirskii</i> (Ślósarski, 1881)	13	15	4.66	0.034	D
EuoStr	<i>Euomphalia strigella</i> (Draparnaud, 1801)	11	17	3.25	0.03	M
ValPul	<i>Vallonia pulchella</i> (O. F. Müller, 1774)	10	53	1.84	0.151	-
EucFul	<i>Euconulus fulvus</i> (O. F. Müller, 1774)	9	14	11.97	< 0.001	W
SucPut	<i>Succinea putris</i> (Linné, 1758)	9	56	11.26	< 0.001	W
ValCos	<i>Vallonia costata</i> (O. F. Müller, 1774)	9	213	9	< 0.001	M
VitCon	<i>Vitrea contracta</i> (Westerlund, 1871)	9	12	6.03	0.017	D
CocLib	<i>Cochlicopa lubricella</i> (Rossmässler, 1835)	8	25	20.11	< 0.001	D
VerMou	<i>Vertigo moulinsiana</i> (Dupuy, 1849)	8	26	9.11	< 0.001	M
SucObl	<i>Succinella oblonga</i> (Draparnaud, 1801)	7	43	6.77	0.001	W
AcaAcu	<i>Acanthinula aculeata</i> (O. F. Müller, 1774)	6	51	2.4	0.079	-
VerSub	<i>Vertigo substriata</i> (Jeffreys, 1833)	6	41	3.12	0.035	M
TroHis	<i>Trochulus hispidus</i> (Linné, 1758)	5	7	not tested		
CarTri	<i>Carychium tridentatum</i> (Risso, 1826)	4	28	(because of low frequency)		
CepVin	<i>Cepaea vindobonensis</i> (A. Férussac, 1821)	4	9			
VitDia	<i>Vitrea diaphana</i> (Studer, 1820)	3	3			
ColEde	<i>Columella edentula</i> (Draparnaud, 1805)	2	3			
AegMin	<i>Aegopinella minor</i> (Stabile, 1864)	1	1			
AriArb	<i>Arianta arbustorum</i> (Linné, 1758)	1	1			
OxyEle	<i>Oxyloma elegans</i> (Risso, 1826)	1	2			

Results

There was a sharp moisture gradient along each transect, with the measured soil moisture varying from 97% in fen plots to 19% in plots located in the surrounding semi-dry grasslands. Soil moisture and calcium content were the most variable factors along the transects, with most of the other measured variables strongly correlating with them (Tables 2, 3). Soil calcium content was extremely high in all samples (Table 2).

Towards wet and calcareous plots in central parts of fens, the percentage cover of moss layer notably increased, whereas herb cover, related with weight of biomass, decreased. The decrease was however somewhat weaker, which resulted in an increase of total plant cover (moss and herb cover together) with soil moisture (Table 3).

Table 2. Descriptive statistic of all variables.

Variables	Minimum	Lower quartile	Mean	Median	Upper quartile	Maximum	Standard deviation
Soil moisture (%)	19	27	61	71	88	97	29
Ca-soil (mg/g)	3.1	13.3	24.4	25.3	36.3	40.7	12.1
N-biomass (%)	0.95	1.19	1.3	1.32	1.41	1.67	0.17
Ca-biomass (%)	0.53	0.79	0.96	0.92	1.08	1.97	0.28
Biomass weight (g)	7.2	13.4	22.3	20.7	27.9	52.1	9.9
Total cover (%)	55	73	84	88	93	100	12
Herb cover (%)	30	60	72	70	80	100	14
Moos cover (%)	0	1	44	40	90	95	39
Nr. of species per plot	2	4	6	5	8	11	2
Nr. of species per site	7	10	14	15	17	17	4
Nr. of live individuals	2	22	70	44	74	922	122

Table 3. Values of Spearman's rank correlation coefficient between environmental variables and their significance. Significant correlations after Bonferroni correction are in bold ($P < 0.00625$).

Variables	Soil moisture		Ca-soil		N-biomass		Ca-biomass		Biomass weight		Total cover		Herb cover	
	rs	P	rs	P	rs	P	rs	P	rs	P	rs	P	rs	P
Ca-soil	0.66	<0.001												
N-biomass	0.03	0.837	-0.2	0.09										
Ca-biomass	0.21	0.116	0.11	0.384	-0.1	0.57								
Biomass weight	-0.5	<0.001	-0.4	0.002	-0.2	0.27	-0.2	0.09						
Total cover	0.43	<0.001	0.43	<0.001	-0.2	0.15	0.22	0.1	0.09	0.492				
Herb cover	-0.5	<0.001	-0.4	<0.001	0.15	0.25	-0.1	0.4	0.7	<0.001	0.3	0.051		
Moss cover	0.82	<0.001	0.75	<0.001	-0.2	0.07	0.27	0.04	-0.3	0.012	0.7	<0.001	-0.3	0.01

Species richness of land snail assemblages varied from 2 to 11 species per plot. Although we expected rather tight response of species richness to soil moisture gradient, only a weak and negative correlation was found (Fig. 1, Table 4). After a Bonferroni correction, only two significant correlations remained – proportional representation of species richness was positively correlated with weight of dry biomass and with cover of herb layer (both these variables were closely related; Table 3).

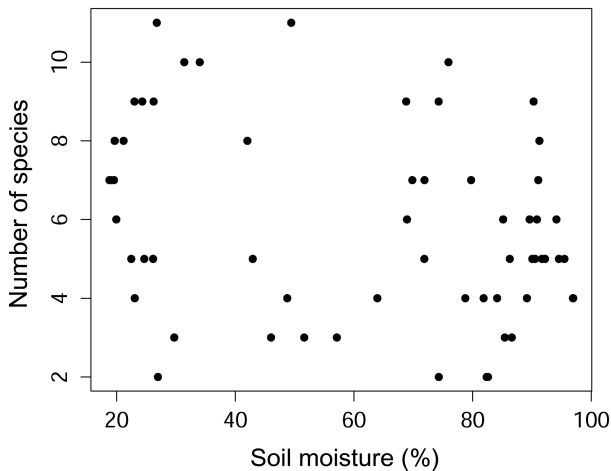


Figure 1. Scatter plot between soil moisture and species richness.

Correlations between both species richness and total abundances and the other variables were not significant (Table 4). We also did not find any non-linear relationship between soil moisture and any measure of species richness and total abundances (data not shown). In contrast, land snail species composition tightly responded to soil moisture gradient, with soil moisture having the highest fit to the first DCA axes (Fig. 2; Table 5). We also found a significant hump-shaped relationship (Chi-square statistic: 59.49 on 2 and 57 DF, approximate $r^2 = 0.273$, $P < 0.002$) between sample scores on the first DCA axes and species richness (Fig. 3).

Table 4. Values of Spearman's rank correlation coefficient between land snail species richness and all environmental variables, and their significance. For detail description see Methods. Significant correlations after Bonferroni correction are in bold ($P < 0.00625$).

Variables	Species richness		Proportional representation		Individuals	
	rs	P	rs	P	rs	P
Soil moisture	-0.28	0.031	-0.24	0.069	-0.08	0.561
Ca-soil	0.09	0.501	0.06	0.639	0.21	0.1
N-biomass	-0.26	0.045	0.05	0.722	-0.24	0.06
Ca-biomass	-0.12	0.363	-0.07	0.595	0.28	0.033
Biomass weight	0.34	0.008	0.38	0.003	0.22	0.094
Total cover	0.12	0.344	0.08	0.56	0.06	0.66
Herb cover	0.3	0.018	0.40	0.001	0.05	0.705
Moss cover	-0.17	0.188	-0.22	0.098	-0.01	0.948

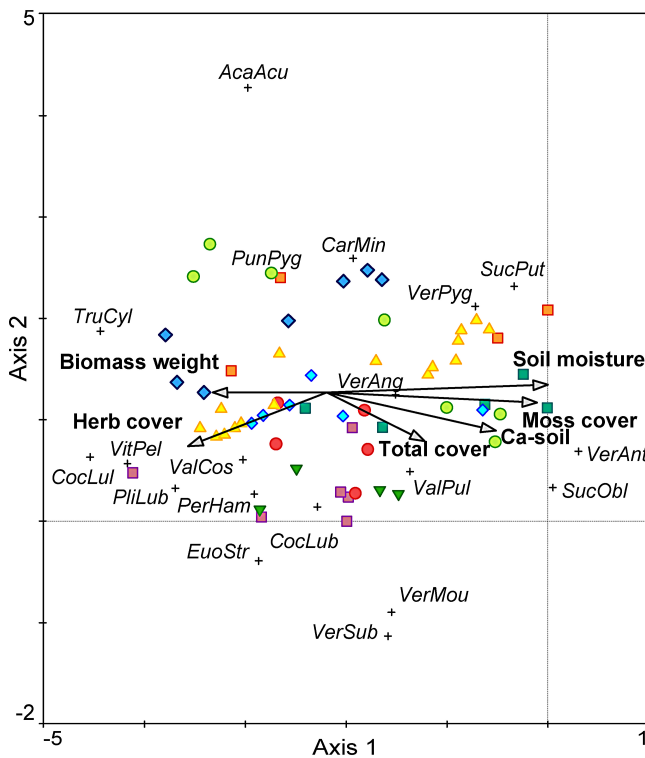


Figure 2. Detrended Correspondence Analysis (DCA) of land snail species data with the site scores on the first two ordination axes. Type of symbols represents individual transects. Species with the higher fit (more than 10%) and only significant variables ($P < 0.01$) were plotted. Eigenvalues: 1st axis = 0.528, 2nd axis = 0.311; explained variation: 1st axis = 15.2%, 2nd axis = 9.0%. For full species names see Table 1.

Among 21 species with the frequency higher than five, 16 showed a significant response to soil moisture; 10 were significant also after a Bonferroni correction (Table 1). Six species expressed affinity to drier plots (i.e., *Cochlicopa lubricella*, *Perpolita hammonis*, *Plicuteria lubomirskii*, *Truncatellina cylindrica*, *Vitrea contracta* and *Vitrina pellucida*), five species were more abundant in moister plots (i.e., *Euconulus fulvus*, *Succinea putris*, *Succinella oblonga*, *Vertigo antivertigo* and *V. pygmaea*), and another five species (i.e., *Carychium minimum*, *Euomphalia strigella*, *Vallonia costata*, *Vertigo moulinsiana* and *V. substriata*) expressed a unimodal response with the preference to intermediate moisture conditions. Several frequent species, such as *Cochlicopa lubrica*, *Punctum pygmaeum* and *Vertigo angustior*, occurred evenly along the whole moisture gradient resulting in a non-significant response (Fig. 4, Table 1).

Table 5. Values of Spearman's rank correlation coefficient between environmental variables and the first two DCA axes, and their significance. Significant correlations after Bonferroni correction are in bold ($P < 0.00625$).

Variables	AX1		AX2	
	rs	P	rs	P
Soil moisture	0.81	<0.001	0.16	0.210
Ca-soil	0.64	<0.001	0.03	0.821
N-biomass	0.16	0.218	-0.11	0.420
Ca-biomass	0.13	0.315	-0.12	0.375
Biomass weight	-0.45	<0.001	-0.01	0.957
Total cover	0.32	0.013	-0.15	0.255
Herb cover	-0.58	<0.001	-0.32	0.013
Moss cover	0.76	<0.001	0.02	0.873

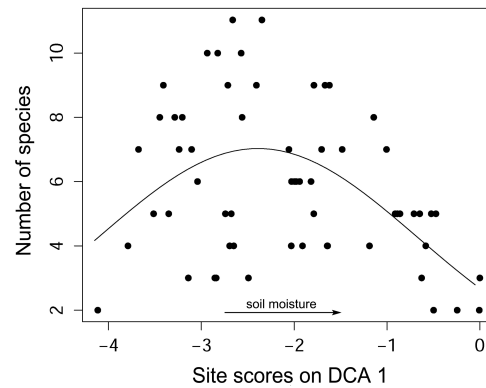


Figure 3. Relationship between site scores on the first DCA axis of snail samples and species richness (GLM, approximate $r^2 = 0.273$, $P < 0.002$).

Discussion

Species richness

Although both species richness and total abundance varied considerably among the plots (Table 2), we have not found any significant relationship between these two variables and soil moisture when species richness was corrected for a site's species pool (Table 4). Aboveground biomass and herb-layer cover were the only significant predictors of proportional species richness, suggesting certain role of vegetation as a shelter and food source for snails (Cook 2001; Dvořáková & Horsák 2012).

Several previous studies exploring effects of soil moisture on land snail species richness documented a positive response, with increasing species richness and/or abundances towards wetter habitats (e.g. Wäreborn 1969; Martin & Sommer 2004a, b). However, it seems that these patterns are site or system specific, related probably also to compound effects of the other environmental variables important for snails, such as soil pH and calcium content in topsoil. For example, Martin & Sommer (2004b) classified sites into few moisture classes and found significant increase of species richness and abundances with increasing site basicity only in intermediate-moist and wettest forest sites. Also dry grassland habitats did not show any significant response of both species richness and total abundances to soil pH (Martin & Sommer 2004a). Getz & Uetz (1994) estimated site moisture using a degree of slope and aspect, and they found a unimodal response of species richness to moisture,

although when sites with low diversity of leaf litter were omitted, a positive linear response was obtained.

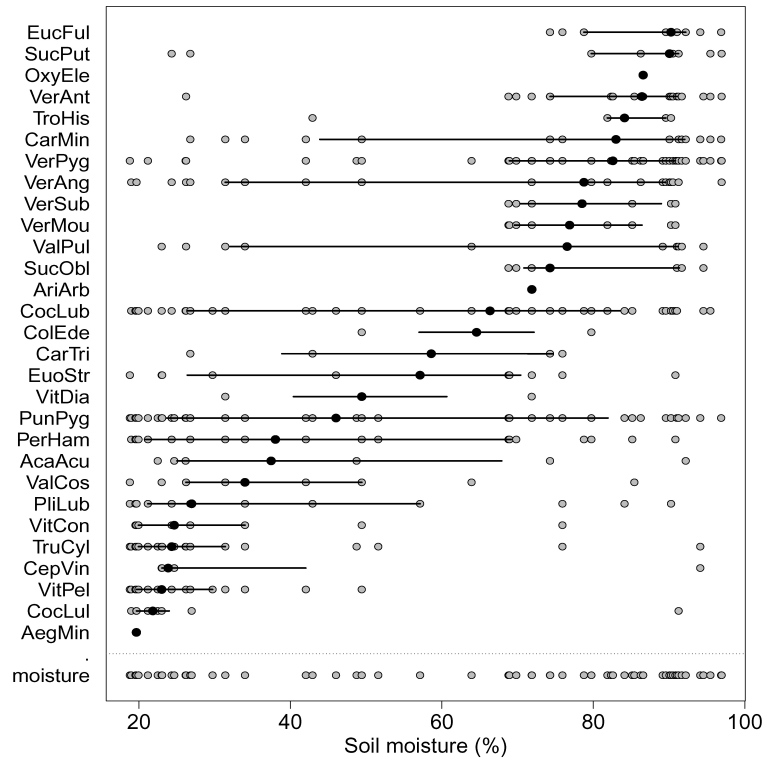


Figure 4. Species occurrences (presence/absence data) along soil moisture gradient. Median (black point), 25–75% quantile (black line) and measured values of moisture where the species occurred (gray point) are displayed. Species are ordered by median values; for full species names see Table 1. Distribution of measured moisture values are shown at the bottom.

It seems that there is no general pattern, especially if looking at ecologically highly different habitats harbouring evolutionary distinct communities. In such a broader-scale overview, we can document species rich assemblages at both rather xeric (e.g. limestone rocks) and humid (e.g. calcareous fens) habitats (Nekola 2002; Horsák & Cernohorsky 2008). Interestingly, even for very straightforward response of snail species richness to the gradient of calcium content, important idiosyncrasies have been recently reported from North American faunas by Nekola (2010). He documented surprisingly species rich assemblages in some acidic habitats harbouring many strictly acidophile land snail species. Nevertheless, at fine scales a tight response of snail species richness to moisture cannot be rejected. Therefore, on the basis of previously published results we expected two possible responses of species richness to soil moisture in our study system – a decreasing linear response toward drier plots or a unimodal hump-shaped pattern with a peak at intermediate values. In contrast, we found only non-significant (after a Bonferroni correction) negative correlation, which can have several possible reasons. First is a lack of permanently dry sites, because the studied grasslands are usually classified as semi-dry. They occur on flysh bedrock, which is rich in clay particles capable of absorbing water and thus keeping moisture in dry periods. This results in a common co-occurrence of both moisture-demanding and dry-grassland plant species (Škodová et al. 2008). We have observed similar patterns for snails as well. For example, several live individuals of wetland snail *Vertigo angustior* was found in a semi-dry grassland approximately 20 m far from the edge of the fen community, though in the study region it is exclusively limited to alkaline wetlands. It illustrates the second reason: dry

grasslands are not spatially isolated from fen communities, and these may act as a part of the source-sink dynamics (Shmida & Ellner 1984). Third, the observed negative correlation between moisture and species richness may be caused by covariation with biomass production. We observed higher biomass production of vascular plants in dry-grassland plots, presumably due to improved nutrient availability as compared to phosphorus-limited fens (Rozbrojová & Hájek 2008). Low-productive vegetation of calcareous fens did not provide suitable shelters for land snail survival during unfavourable periods (Schamp et al. 2010) and is probably also less palatable because of prevalence of sedges over herbs and grasses (Schamp et al. 2011).

Species composition

In contrast to species richness and abundances, we observed remarkable change of species composition over the gradient. Particular species differed in their optima along the gradient, with five species (after a Bonferroni correction, Table 1) preferring wetter plots, other three species being more abundant in drier plots. Only two species experienced a unimodal response, though their optima were shifted towards wetter (*Vertigo moulinsiana*) or drier (*Vallonia costata*) plots. This clearly suggests a species turnover from drier to wetter plots rather than species accumulation towards wetter plots. Similar result was found in the Danube floodplain forests, from where Čejka et al. (2008) reported a great effect of moisture on snail species composition, but not on species richness and total abundances. Chiba (2007) reported the coincidence between moisture and snail species richness as well, but contrary to our study, he also found a hump-shaped relationship between moisture and species richness. However, he did not measure or estimate moisture, but used the first DCA axis as its proxy. We can demonstrate how this approach may be misleading. In concordance, our data also clearly show a hump-shaped relationship between the species richness and the plot scores on the first DCA axis (Fig. 3), which was tightly associated with soil moisture (Table 5). Despite that, there was no significant relationship between moisture and any measure of species richness in our study. This pattern thus seems to be driven by a confounding effect of a fine-scale species turnover associated with the well-known concept of ecotone (or rather ecocline in our study system), where species common to the adjacent assemblages are allowed to coexist (see van der Maarel 1990). Such samples are inherently placed in the middle of the ordination axis, as their species composition results from meeting faunas of different ecologies, although they may not necessarily have intermediate values of soil moisture.

Species responses

Using species response modelling, we obtained more or less different autecological conclusions for some species than was previously published from different habitats (Martin & Sommer 2004b; Čejka & Hamerlík 2009) and even from the same habitat sampled in a wider area and higher number of sites (Horsák et al. 2007). However, it is important to stress that these results are hardly comparable. In the three above-mentioned studies, only one sample per study site was sampled, and ecological variation among the sites was much higher. The results can be further biased by confounding factors and biotic interactions. We therefore assume that our within-site design could at least partially control for some of these drawbacks of the traditional sampling scheme. Despite these circumstances, there were several species that expressed consistent response across different studies. *Vallonia costata*, for example, was always more common in drier plots. In addition, our autecological results are identical with those of Martin & Sommer (2004a), who sampled similar habitats using similar sampling scheme, that is, sampling in separate sites, but in a distinct region, which was homogeneous with respect to climate and environment characteristics.

Conclusions

In this study, we used the within-site sampling design to control for confounding effects other than soil moisture, which was measured directly. Even if moisture correlated with soil calcium in our sites, the amount of calcium was very high in all plots, making the effects of its variation for land-snail composition negligible (Horsák 2006). Using this methodology, we observed clear compositional changes along the moisture gradient, suggesting differences in species preference to soil moisture conditions even at a fine, within-site scale. Species richness did not change, or changed slightly negatively, along the gradient. Although some of these results can be explained either by missing extremely dry plots or by specific features of our study system, it suggests that the effect of soil moisture on land snail communities is rather variable across ecologically different habitats and geographically and evolutionary distinct faunas.

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Changes in species richness and species composition of vascular plants and bryophytes along a moisture gradient

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Abstract

We focused on the gradient in moisture along transects of from 8 to 30 metres in length from spring fen to semi-dry grassland vegetation. We selected an area in the calcium-rich part of the Western Carpathian flysch zone (Czech and Slovak Republics) where small spring-fed fens occur in close contact with semi-dry grasslands. Altogether 126 vegetation plots of 75 x 75 cm were sampled along 15 transects (one per locality) that each extended from the wettest part of a spring-fed fen into the surrounding semi-dry grassland. In addition, samples of standing plant biomass and soils were analyzed for nutrients (N, P, K, C, Ca) and the upper-soil moisture measured. Using this study system and these sampling methods, we can test directly the effects of moisture and so avoid the confounding effects of different background environmental conditions that occur when data from many distinct sites is used. Data were processed using linear mixed-effect models and other statistical techniques. The trend in the number of species of vascular plant was unimodal with the optimum skewed towards lower moisture values. This response was not caused by an edge effect alone as replacing the moisture gradient with the positions of plots on transects resulted in a much weaker unimodal relationship and there is a group of species that occurred mainly in the species-richest moderately moist plots but do not occur in fens or the driest grasslands. The correlations between species richness and productivity (positive) and soil calcium (negative) differ from most of those reported in the literature, which suggests that the observed relationship between species richness and moisture is probably not greatly confounded by these factors. Species richness correlated negatively and the percentage of endangered species positively with the N:P biomass ratio, which is in accordance with other published results, but their correlations with moisture were stronger. For bryophytes, species richness linearly decreased towards the dry plots and did not correlate with any of the nutrients measured. Most of the species of vascular plants and bryophytes in the wettest patches were fen specialists, while more generalists made up the species richness in grasslands, including the species-richest patches. For bryophytes, the percentage of specialists was very high in fen plots. Although Mantel tests showed that bryophyte and vascular plant species turnovers were similar, we recorded substantial differences in their species richness patterns. Comparison with the results of a previous study on molluscs revealed a greater similarity between bryophytes and molluscs than between them and vascular plants in terms of correlations between species richness and environmental variables. We argue that soil moisture should be taken into account when explaining current patterns in diversity in extremely-rich temperate grasslands.

Key words: *Caricion davallianae*, *Festuco-Brometea*, nutrients, productivity, semi-dry grassland, specialist, species density, spring fen, transect, White Carpathians

Introduction

Soil moisture is one of the most important environmental factors affecting plant species physiognomy and physiology and, as a consequence, species composition and diversity of plant communities. The variation in species richness along a moisture gradient is much less often recorded than the variation along gradients in terms of pH, productivity or availability of nutrients (for the most recent studies see, e.g. Cachovanová et al. 2012, Güssewell et al. 2012, Merunková & Chytrý 2012, Araya et al. 2013, Klaus et al. 2013, Kuiters 2013).

The variation in species richness along gradients of moisture are recorded predominantly for floodplain or riparian vegetation (e.g. Wassen et al. 2002, Dwire et al. 2004, Loheide & Gorelick 2007) and within mires (Navrátilová et al. 2006, Jabłońska et al. 2011). Studies along small-scale spatial gradients and on species-rich semi-terrestrial vegetation are rare (e.g. Flintrop 1994, Zelnik & Čarni 2008, Williams et al. 2011). We therefore selected a calcareous area in the Western Carpathian flysch zone, where small fens occur in close proximity with moist, semi-dry and dry grasslands and therefore the effect of moisture can be studied along rather long gradients (Hettenbergerová & Hájek 2011, Schamp et al. 2011, Hettenbergerová et al. 2013). Spring-fed fens in that area belong to threatened Central-European habitats because of their small area and specific environmental conditions. Despite their small area, they harbour a high number of endangered species for which their exact dependence on the level of moisture is unknown. Further, carrying out this research in this region has another advantage. White Carpathian semi-dry grasslands are famous for their extremely species-rich grasslands (Klimeš et al. 2001, Wilson et al. 2012), which results from their history (Hájková et al. 2011) and a unique combination of abiotic factors and management (Merunková et al. 2012). While some authors (Klimeš 2008, Merunková et al. 2012) have speculated that the high species richness of some Carpathian grasslands is determined by intermediate moisture levels, no study has directly tested the species richness-moisture relationships along a long moisture gradient in this region.

Not only high levels of moisture, but also low availability of nutrients may explain the occurrence of rare species in calcareous fens (Wassen et al. 2005). In the White Carpathians there are high levels of calcium carbonate in tufa-forming spring-fed fens, which accounts for the low availability of phosphorus for vascular plants growing in these fens (Rozbrojová & Hájek 2008). There are species that can survive in these extreme ecological conditions for which each fen is an island refuge in an otherwise rather dry landscape (Horsák et al. 2012, Kapfer et al. 2012). Low availability of nutrients and permanent high ground-water level determine the high biomass of bryophytes growing in these fens (Hájková & Hájek 2003), whereas the semi-dry grasslands are dominated by vascular plants (Škodová et al. 2011). It is, therefore, possible to compare the moisture driven diversity patterns for two contrasting taxonomic groups. Only a few studies have directly compared the response of more groups of organisms, sampled in the same plots, to the moisture gradient. Such comparisons lead to more general conclusions about the relationships between soil moisture and biological diversity. In a previous study on the same system the moisture driven diversity pattern of molluscs was studied (Dvořáková & Horsák 2012 within semi-dry grasslands; Hettenbergerová et al. 2013 along the fen-to-grassland gradient). Patterns in bryophyte, vascular plant and mollusc species composition and richness along a moisture gradient have not been previously directly compared. Generally speaking, bryophytes and vascular plants in fens are more often compared with respect to the pH/calcium gradient (Hájek et al. 2011, Sekulová et al. 2011, 2012) than the moisture gradient. The expectation is that their behaviour with respect to moisture will differ in terms of traits such as body size, type of reproduction, propagule dispersal, nutrient uptake and water use efficiency (Kapfer et al. 2012, Street et al. 2012).

The main questions addressed in this study were: (1) how does species richness and species composition of vascular plants and bryophytes change along a gradient of moisture from semi-dry grasslands to spring-fed fens? (2) Which environmental factors are correlated with the fen-to-grassland gradient? (3) Is there any difference between the species richness and species composition patterns of vascular plants, bryophytes and molluscs (identified in a previous study)? (4) Is high species richness determined more by the numbers specialists or generalists?

Study area

The study area is situated on the border between the Czech and Slovak Republics in the White Carpathian Mountains and Vsetínské Mountains, which are a part of the Outer West Carpathians. The localities are at altitudes between 330 and 550 m a.s.l. Annual mean temperature in this area is about 7.5 °C and annual mean precipitation is approximately 700 mm. The bedrock in this area is formed by flysch, which is composed of alternating clay stones and sandstones, which means it is possible to have wetland and semi-dry grassland communities close to together. The localities were chosen in order to have as long as possible within-site gradient in moisture. At each locality there was a steep gradient in moisture from the fen to the semi-dry grassland. The vegetation in the fens belonged to the *Caricion davallianae* alliance and that in the surrounding semi-dry grasslands to the *Festuco-Brometea* class (alliance *Cirsio-Brachypodium pinnati* or *Bromion erecti*). Ecotonal communities classified within *Calthion* alliance occurred at some localities between fens and grasslands.

Nomenclature of the vegetation follows Chytrý (2007, 2011), that of vascular plants follows Danihelka et al. (2012) and of bryophytes Kučera et al. (2012).

Material and methods

Field sampling and environmental variables

Field data were collected in June and July during the years 2005–2008. At each of 15 localities one linear transect extended from the moistest part of the spring fen into the semi-dry grassland surrounding the fen with its central part in the transitional zone between fen and grassland. This zone in all cases was rather narrow and easily visible in the field as a structural ecotone, i.e. a steep transition between sedge-moss vegetation on wet soil to herbaceous plant-grass vegetation on dry soil. The number of plots sampled along each transect ranged from 5 to 16 and depended on the area of the fen. Altogether 126 plots were sampled. The size of plots was 75 x 75 cm and the distance between the centres of two neighbouring plots was two meters.

In each plot, species cover was estimated using a nine-grade scale (van der Maarel 1979). Both vascular plants and bryophytes were recorded. To obtain more information about nutrient limitations a sample of standing vascular plant biomass was taken from a 25 x 25 cm subplot in the centre of each plot. An upper soil sample was also taken. Moisture in the upper layer of the soil horizon (approximately 10 cm) was measured in each plot, always throughout the study area during a dry summer period (between July and September), using a moisture meter (ThetaProbe, soil moisture sensor ML2x). Concentrations of nitrogen, phosphorus, potassium and calcium in the dried and weighed vascular plant biomass were subsequently analyzed; concentration of calcium and organic carbon were determined in soil samples. Before the chemical analyses, the samples of vascular plant biomass were air-dried at 70 °C. For the nitrogen determination, dry material was mineralised with sulphuric acid and hydrogen peroxide, and the nitrogen concentration determined by the distilling method using a Kjeltec apparatus. For determination of the other elements, material was mineralised in a sealed system, using microwave heating. Phosphorus concentration was determined spectrophotometrically, potassium concentration by atomic emission spectrophotometry and

that of calcium by atomic absorption spectrophotometry (Zbírál 1994). Plant-available calcium in the soil was extracted using the Mehlich III (strong acid extraction with ion complex) method and determined using atomic absorption spectrophotometry. Organic carbon was determined by gravimetry (Zbírál 1995). Soil pH was not measured in these analyses because the range of values was too narrow ($\text{pH}_{\text{H}_2\text{O}}$ 6.0–8.0) as the soils in all the plots were base rich.

Data analysis

Relationships between species richness and the variables measured were statistically analyzed using Spearman's rank correlation coefficient. A Bonferroni correction was used to correct for the problem associated with multiple testing. Relationships between particular environmental variables were evaluated using principal component analysis (PCA), applied to centered and standardised variables. Relationship between species richness (of vascular plants or bryophytes, respectively) and soil moisture measurements was evaluated using linear mixed-effect models, where soil moisture was included as quantitative fixed effect and locality (i.e. the transect) as a random effect. Both linear and polynomial types of relationship between species number and moisture were modelled and tested against each other to decide whether the shape of the relationship is linear or unimodal. To determine whether there is an edge effect on species richness, we analyzed the relationship between number of species and standardized position of a plot along a transect. The plot positions along a transect were standardised to zero mean and unit variance in which the central plot, located on the fen-grassland transition, had a zero value, semi-dry grassland plots negative and fen plots positive values. The relationship was also analyzed using linear mixed-effect models, in which the standardized position of a plot along a transect was included as a quantitative fixed effect and identity to locality (i.e. the transect) as a random effect. Both the linear and polynomial types of relationship were again tested against each other to determine the shape of the relationship.

Both the specialist vascular plants and bryophytes were selected using lists of diagnostic species for target alliances and associations obtained from the analysis of a large vegetation-plot database for the Czech Republic in the Vegetation of the Czech Republic monograph (Chytrý et al. 2007, 2011). Thirty-eight species diagnostic for the *Scheuchzeria palustris*-*Caricetea nigrae* class, *Caricion davallianae* alliance and the *Valeriano dioicae*-*Caricetum davallianae* and *Carici flavae*-*Cratoneuretum filicini* associations were considered to be fen specialists, whereas 60 species diagnostic of the *Festuco-Brometea* class, *Bromion erecti* and *Cirsio-Brachypodium pinnati* alliances and *Brachypodio pinnati*-*Molinietum arundinaceae* and *Scabioso ochroleucae*-*Brachypodietum pinnati* associations were considered to be semi-dry grassland specialists. One species, *Molinia arundinacea* s. s. (see Dančák et al. 2012 for taxonomic concept), was excluded from the semi-dry grasslands specialists because in the study area it occurs frequently also in fens. For the 181 remaining species was used the term "generalists". The relationship between percentage of specialists in the vegetation and moisture level was analyzed using linear mixed-effect models (moisture a quantitative fixed effect and identity to locality a random effect). Only the linear regression model was tested, as testing polynomial model lacks theoretical justification. Relationships between number of specialist species and environmental variables were analyzed using Spearman's rank correlation test with a Bonferroni correction. In the same way we analyzed also the species richness and percentage of endangered species (categories C1–C4 in Grulich 2012).

Main ecological gradients were determined using detrended correspondence analysis (DCA) of square-root transformed data. Similarity between vascular plant and bryophyte matrices were compared using a Mantel test with square-root transformation based on Bray-Curtis distance and 999 permutations. Using data for the same 60 plots obtained in a previous malacological study (Hettenbergerová et al. 2013) we compared gradients of three

different taxonomic groups: vascular plants, bryophytes and molluscs using a Mantel test based on the log-transformed data. All analyses were computed using the R program (version 2.15.2, R Core Team 2012).

Results

The soil moisture varied along the gradient studied (Electronic Appendix 1) from 18.8% in semi-dry grassland plots to 98.28% in fen plots. Vascular plant total species richness ranged from 8 to 53 species per plot, number of bryophyte species was between 0 and 13 per plot (Electronic Appendix 1). Regarding the relationship between number of vascular plant species and moisture, the polynomial model performed significantly better than the linear model ($p < 0.001$) and the polynomial model was significant ($p < 0.001$, Fig. 1) and had a unimodal shape with optimum shifted towards lower moisture values. The lowest species richness was recorded in the wettest plots, while the highest numbers of species were recorded in plots with intermediate-low moisture levels (37–60%). There were four maximum values for total number of bryophyte species over the same moisture range, but the general species richness-moisture relationship modelled using mixed-effect models was linear with a decrease towards dry plots ($p < 0.01$; Fig. 1). The polynomial model in this case was not significantly better than the linear one ($p = 0.078$). When the relationship between number of species and standardized plot position, (i.e. the effect of the structural ecotone visible in the field) was tested, the relationship for vascular plants was unimodal (Fig. 2), although less clear than that of species richness along the moisture gradient, with the polynomial model significantly better than the linear ($p < 0.05$) and overall significant ($p < 0.001$). In the case of bryophytes the relationship was linear (overall significance of linear model $p < 0.05$, with polynomial model not significantly better with a value of $p = 0.148$).

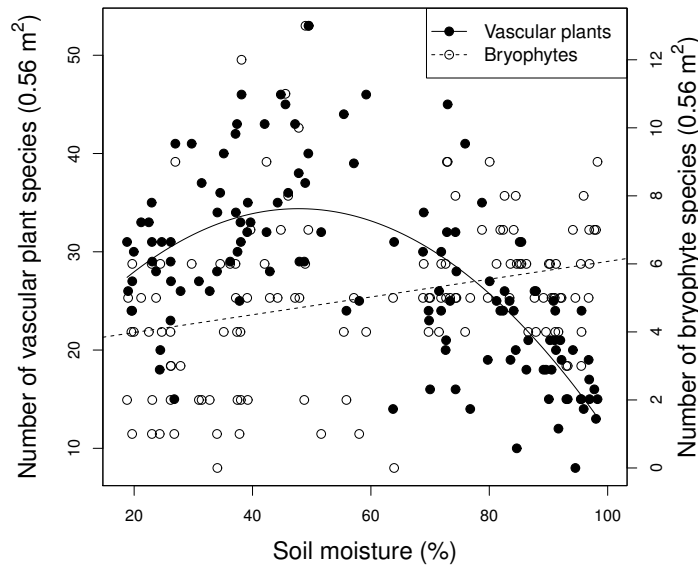


Figure 1. Relationships between species richness of vascular plants and bryophytes and soil moisture. The regression for vascular plants was fitted using polynomial and for bryophytes using linear regression.

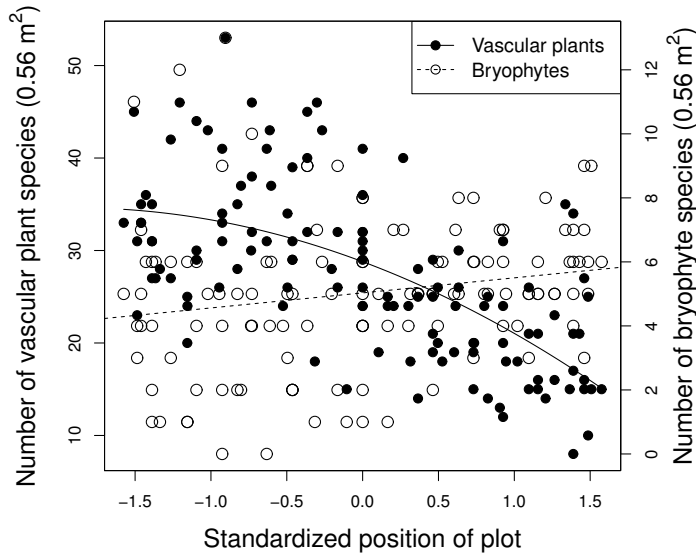


Figure 2. Relationship between species richness of vascular plants and bryophytes and the standardized position of the plots along the transects. Negative values refer to semi-dry grasslands and positive values to spring fens. The regression for vascular plants was fitted using polynomial and for bryophytes linear regression.

Total species richness of vascular plants correlated also with the amount of calcium in the soil, weight of biomass (i.e. productivity) and biomass N:P and N:K ratios (Table 1). Nevertheless, all these variables correlated also with soil moisture (see Electronic Appendix 2 and 3). Number of semi-dry grassland specialist species correlated with the same environmental variables as total species richness. Fen specialist species richness showed opposite correlations compared to total species richness. Number of bryophyte species was positively significantly associated only with soil moisture, but number of fen bryophyte specialists was positively also associated with soil calcium and N:K ratio and negatively with weight of vascular plant biomass. Semi-dry grassland bryophyte specialist species richness was negatively associated with soil moisture, soil calcium and biomass N:P and N:K ratios (Table 1).

Table 1. Values of Spearman rank correlations between species richness and the variables measured and their statistical significance. Significant correlations after Bonferroni correction are in bold ($P < 0.00714$).

	Number of vascular plant species						Number of bryophyte species					
	All species		Semi-dry grassland specialists		Spring fen specialists		All species		Semi-dry grassland specialists		Spring fen specialists	
	rs	P	rs	P	rs	P	rs	P	rs	P	rs	P
Soil												
Moisture	-0.57	<0.001	-0.78	<0.001	0.76	<0.001	0.34	<0.001	-0.45	<0.001	0.79	<0.001
C	0.09	0.294	-0.11	0.241	0.09	0.335	0.1	0.251	-0.12	0.172	0.12	0.17
Ca	-0.66	<0.001	-0.7	<0.001	0.62	<0.001	0.02	0.805	-0.5	<0.001	0.6	<0.001
Biomass												
Weight	0.39	<0.001	0.34	<0.001	-0.21	0.02	-0.18	0.05	0.1	0.273	-0.34	<0.001
Ca	0.14	0.128	0.19	0.034	-0.09	0.297	0.13	0.153	0.23	0.009	0.04	0.697
N:P	-0.5	<0.001	-0.27	0.002	0.32	<0.001	-0.08	0.4	-0.26	0.003	0.24	0.007
N:K	-0.49	<0.001	-0.41	<0.001	0.29	<0.001	0.02	0.863	-0.26	0.003	0.25	0.004

Most of the vascular plant species recorded in the wettest patches were fen specialists (Fig. 3a) and the number significantly linearly decreased towards the dry patches ($p < 0.001$, Fig. 4). Only a few generalist or semi-dry grassland specialists occurred in fens. On the other hand, the high species richness in intermediate and dry plots is made up of not only semi-dry grassland specialists but also generalists. Bryophytes showed a similar and even more clear pattern ($p < 0.001$, Fig. 3b and 4), but there was only a small number of semi-dry grassland specialists. The species richness of endangered species of vascular plants correlated (Spearman rank correlation; $P < 0.00714$ after Bonferroni correction) only with soil moisture ($r_s = 0.403$), while percentage of endangered species correlated with soil moisture ($r_s = 0.648$), soil calcium ($r_s = 0.431$), N:P biomass ratio ($r_s = 0.346$), N:K biomass ratio ($r_s = 0.302$) and also with vascular plant species richness ($r_s = -0.402$).

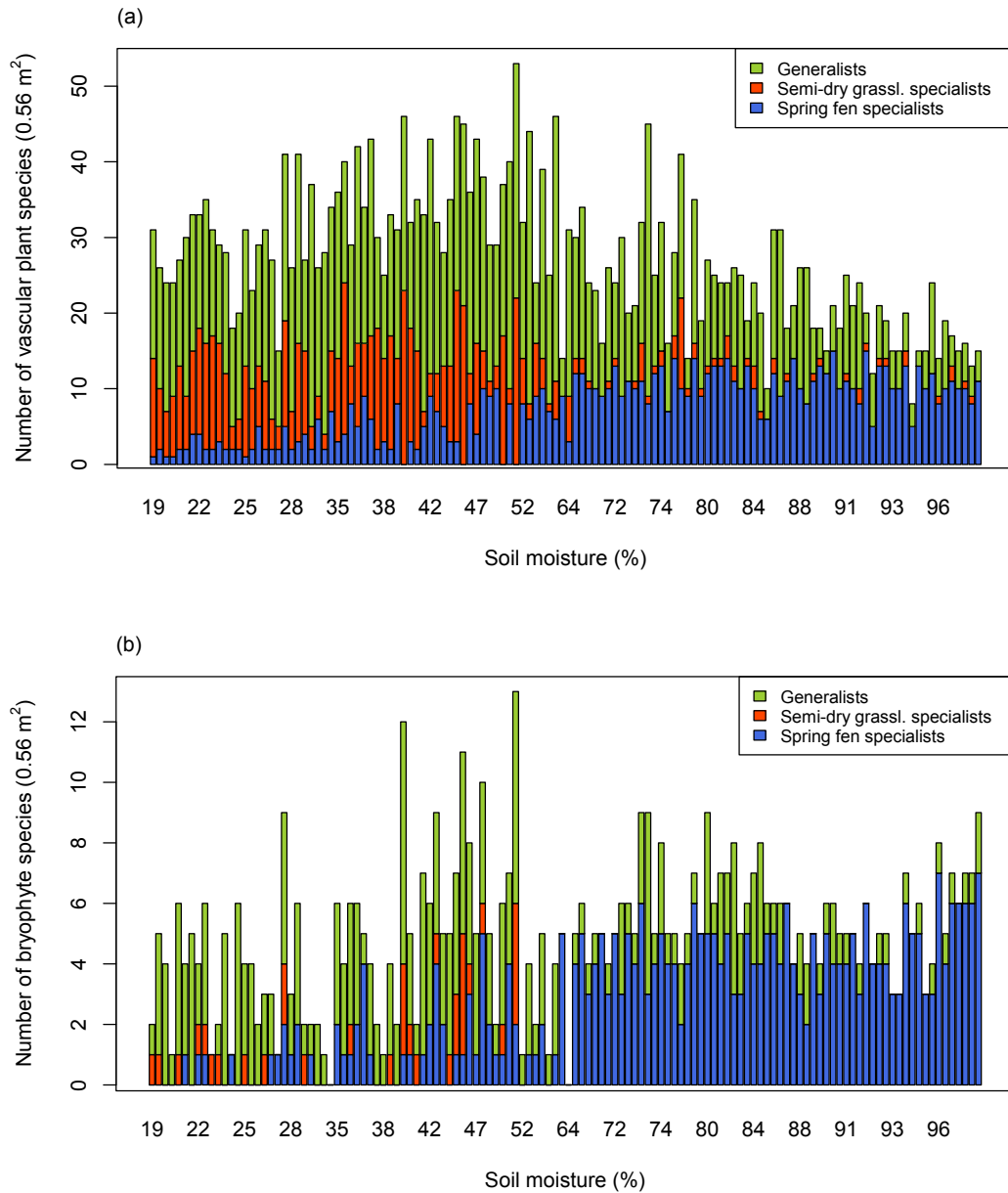


Figure 3. Numbers of species of vascular plants (a) and bryophytes (b). Each column represents one plot on the soil moisture gradient.

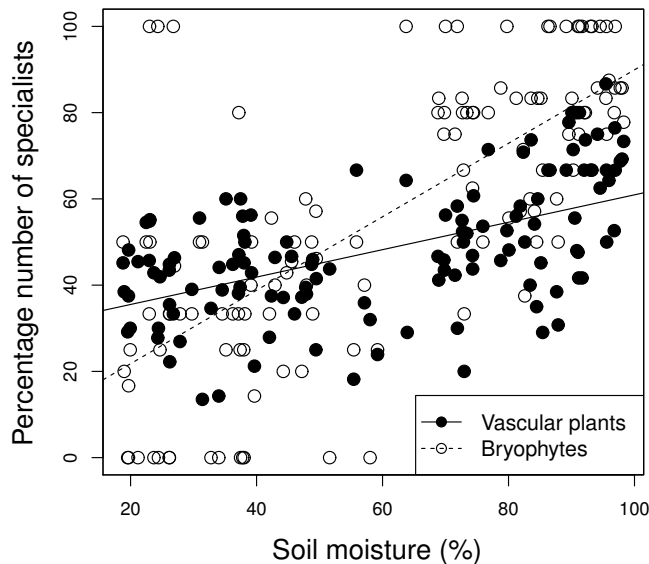
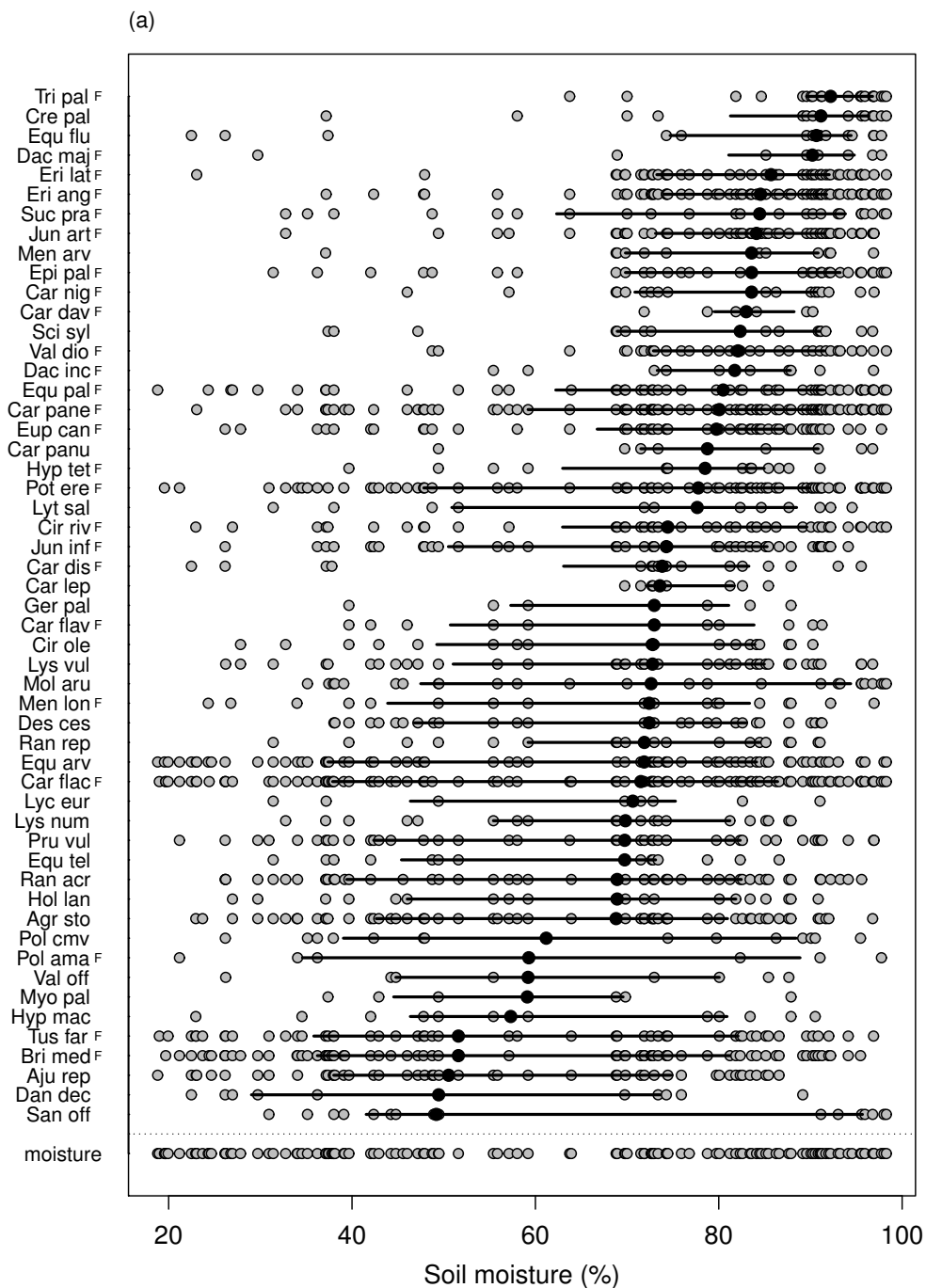


Figure 4. Relationship between percentage of the species that are specialists and soil moisture.

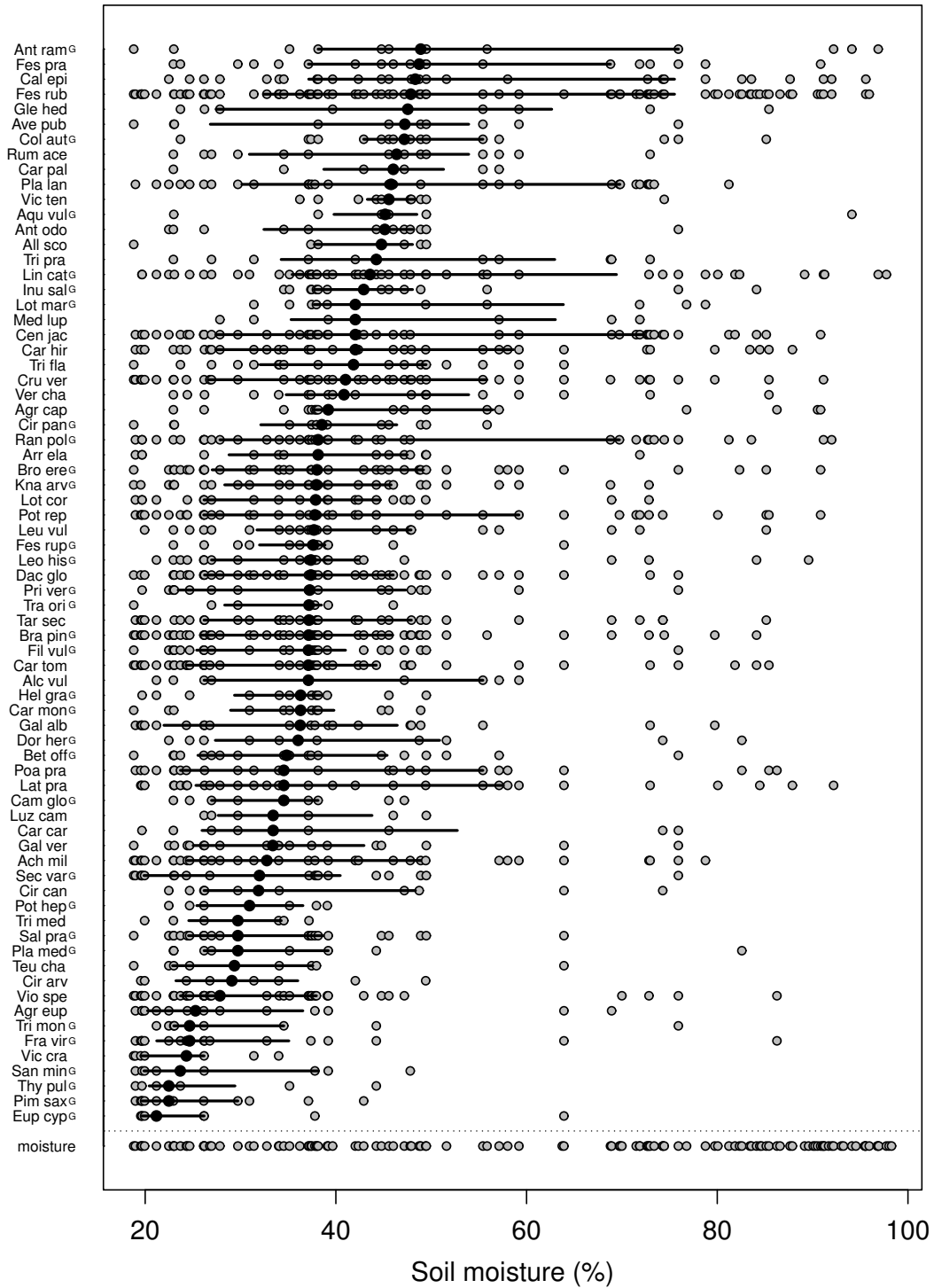
For each species we described its distribution pattern along the moisture gradient (Fig. 5). The most common species occurring along the whole moisture gradient were *Carex flacca* (recorded in 95 of the 126 plots), *Calliergonella cuspidata* (89) and *Festuca rubra* (84); other common species were *Equisetum arvense* (73), *Briza media* (69), *Plagiomnium affine* agg. (63) and *Tussilago farfara* (51). Species that occurred mainly in wet fen plots were fen specialists (e.g. *Triglochin palustre*, *Dactylorhiza majalis*, *Eriophorum angustifolium*, *E. latifolium*; *Philonotis calcarea*, *Palustriella commutata*, *Aneura pinguis*) and species that are not considered to be strict fen specialists and occur in many wetland habitats (*Crepis paludosa*, *Equisetum fluviatile*, *Mentha arvensis*). On the other hand, species that occurred mainly in the driest patches belong mostly to semi-dry grassland specialists (*Euphorbia cyparissias*, *Pimpinella saxifraga*, *Thymus pulegioides*, *Sanguisorba minor*; *Homalothecium lutescens*, *Fissidens dubius*). Some fen specialists, i.e. the species used as diagnostic of calcareous fen vegetation in Chytrý (2011), occurred along the entire moisture gradient (e.g. *Potentilla erecta*, *Carex flacca*, *Tussilago farfara*, *Briza media*; *Calliergonella cuspidata*).

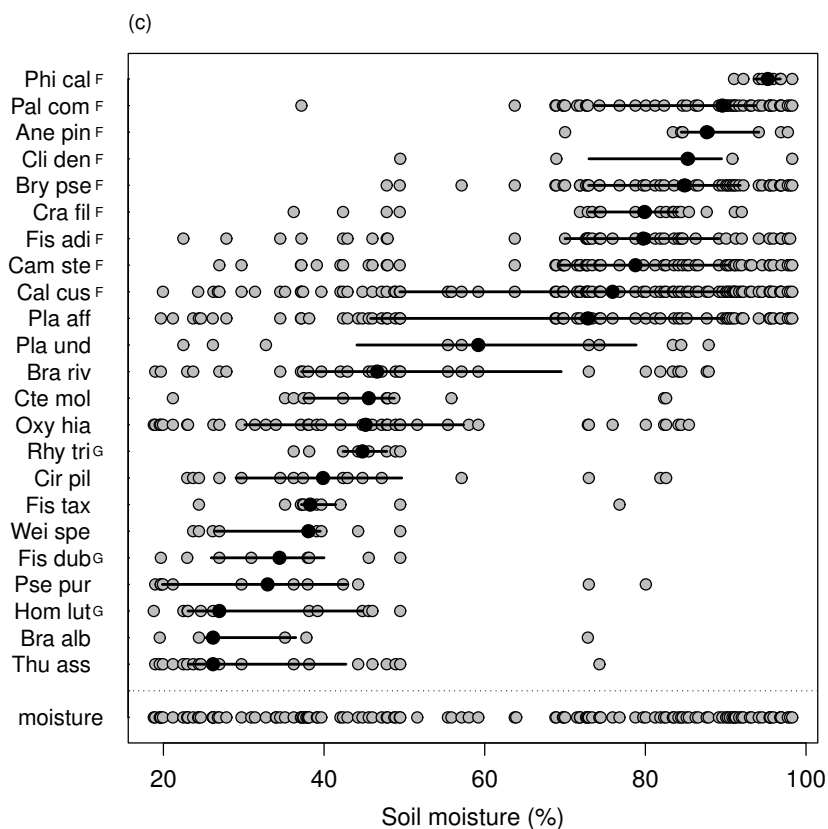
Only a few species had median values for moisture (calculated from the moisture measured at sites of their occurrence) between 50–70%, and all of them showed wide distribution along the moisture gradient (Fig. 6). There was a single species (*Carex lepidocarpa*) with median moisture between 50–80% and, simultaneously, with interquartile range less than 20%. On the other hand very few species had middle median value and low interquartile range (Fig. 6). A group of species that inhabited grasslands and not fens occurred mainly in species-richest plots of rather intermediate moisture of between 37–60% (*Aquilegia vulgaris*, *Allium scorodoprasum*, *Anthoxanthum odoratum*, *Carex pallescens*, *Colchicum autumnale*, *Inula salicina*, *Rumex acetosa*, *Vicia tenuifolia*; *Ctenidium molluscum*, *Fissidens taxifolius*, *Rhytidiadelphus triquetrus*).

Figure 5. Occurrence of species of vascular plants (a, b) and bryophytes (c) along the soil moisture gradient. Median (black point), 25–75% quantile (interquartile, black line) and soil moisture measured where the species occurred (grey point) are displayed. Species are ordered by median values; for full species names see Electronic Appendix 4. Letter at the end of the abbreviation refers to either spring fen (F) or semi-dry grassland (G) specialists. Only species with a frequency > 6 and presence on two or more transects are displayed. Distribution of moisture values are shown at the bottom of the figure.



(b)





Remarkable changes in species composition of vascular plants and bryophytes were recorded along the moisture gradient. The species turnover from drier to wetter plots was high (the length of first DCA axis for vascular plants = 4.090 SD, for bryophytes = 2.776 SD). Mantel test revealed a highly significant correlation ($r = 0.561$, $p < 0.001$) between both vascular plant and bryophyte abundance matrices. Mantel test based only on 60 malacological plots showed in all three combinations of taxonomic groups highly significant relationships (vascular plants versus bryophytes: $r = 0.600$, $p < 0.001$, vascular plants versus molluscs: $r = 0.542$, $p < 0.001$, bryophytes versus molluscs: $r = 0.370$, $p < 0.001$).

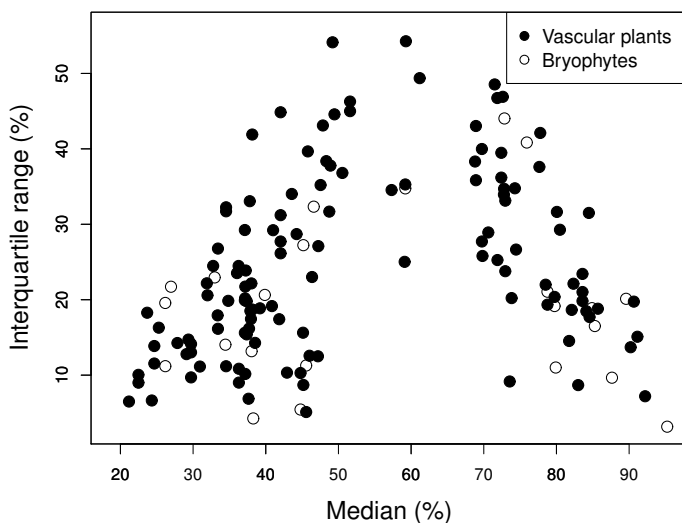


Figure 6. Relationship between median and interquartile range (for values see Fig. 5) for particular species of vascular plants and bryophytes.

Discussion

The effect of moisture and possible confounding factors

The results confirmed our preliminary hypothesis that there would be more species of vascular plants and fewer species of bryophytes in semi-dry grasslands than fens (see also Hájková & Hájek 2003). However, the trend in the number of species of vascular plants did not peak in the driest parts of the grasslands, but was unimodal. This unimodal trend seems to be largely due to the effect of moisture *per se* and not an edge effect, which is frequently reported in the interface between forests and grasslands (Łuczaj & Sadowska 1997, Orczewska & Glista 2005) or between wetland and arid habitats (Hou et al. 2008). This presumption is supported by two pieces of evidence. First, there was only a weak and marginally significant unimodal relationship when a standardized plot position is used as an independent variable. Second, the occurrence of the group of species that characterize the richest plots was confined to particular moisture levels. The lack of an edge effect in the system studied (see also Hettenbergerová & Hájek 2011 for further evidence) refutes the hypothesis of Merunková et al. (2012) that source-sink dynamics in fen-grassland mosaics have a role in determining the high species richness of grasslands in the White Carpathians. Our results rather support the hypothesis that intermediate or fluctuating moisture levels have a role in determining high local species richness in these grasslands, where mesophilous and moisture-demanding species co-exist with xerophilous species (Klimeš 2008, Škodová et al. 2011, Merunková et al. 2012). At the extreme ends of the moisture gradient, species richness is restricted either by anoxia (fens) or seasonal drought (the driest grasslands).

The observed trend of species richness along the gradient of moisture does not appear to be affected by the confounding effects of different background environmental conditions when data for many distinct sites are used, which conforms to the results of a previous study on molluscs (Hettenbergerová et al. 2013). Although moisture and some of the other factors are inter-correlated, the correlations with moisture best explain the observed pattern in species distribution. Soil pH, the principal determining factor in many large-scale studies (Pärtel 2002), was similar in all the plots. Soil calcium correlated negatively with species richness in some cases, while in general the correlations between calcium and species richness are positive (Pärtel 2002, Cachovanová et al. 2012, Merunková & Chytrý 2012, Sekulová et al. 2012). Taking into consideration that the concentration of calcium along the entire moisture gradient was rather high (see also Hettenbergerová et al. 2013) we conclude that the result for calcium is because the values for calcium and moisture co-vary. In species-poor fens calcium is continuously supplied by spring water, while in surrounding grasslands calcium is slightly leached from the topsoil.

Also the correlation with productivity (biomass weight) is because it and moisture co-vary. We found a positive correlation between species richness and productivity, whereas most studies from analogous productivity levels record either no or a negative correlation (Vermeer & Berendse 1983, Wheeler & Shaw 1991, Bergamini et al. 2001, Hájková & Hájek 2003; but see Olde Venterink et al. 2001). The relationship between species richness and moisture recorded in our study conforms with the results of Dwire et al. (2004), who report a high species richness in dry grasslands and low species richness in wet grasslands, but the aboveground plant biomass correlated positively with moisture in Dwire's study and negatively in our study.

On the other hand, we cannot distinguish between the causal effects of moisture and phosphorus limitation on the species richness pattern. High N:P ratios, which we recorded mainly in fen grasslands, generally is inconsistently correlated with species richness (Güsewell 2004). Güsewell et al. (2005) record low species richness at sites with a high N:P ratio, as occurred in our study. That a high percentage of the species at sites with a high N:P are endangered corresponds with the results of studies by Wassen et al. (2005) and

Pawlikowski et al. (2013, this issue), but the much stronger correlation with moisture recorded in our study suggests that the effect of moisture is more important. The complexity of the relationship between moisture, phosphorus limitation and species richness is highlighted by the causal relationship between moisture and phosphorus availability. The high amount of calcium carbonate in our fen grasslands makes phosphorus unavailable (Boyer & Wheeler 1989, Rozbrojová & Hájek 2008).

Distribution of specialists

The stress caused by both phosphorus limitation and anoxia due to high water levels in general favour specialists in fens while in drier grasslands competition favours generalists. Analogous results are reported by Zelnik & Čarni (2008) who record the same pattern for S-strategy and C-strategy species. The former correspond largely to specialists and the latter to generalists.

Based on an analysis of a large database, Fajmonová et al. (2013) report that there is a statistically significant overrepresentation of plant specialists in spring-fed fens and semi-dry grasslands in the Outer Carpathians, both of which were included in our study. The percentage of specialists in semi-dry grasslands was roughly equal to that in spring-fed fens. This discrepancy with our results is attributed to the different methods used to identify the specialist and different scales used in these two studies. The use of small plots in our study probably resulted in an overestimate of local environmental filtering over species pool effects, which were more important in the study of Fajmonová et al. (2013). Further, our result that the species richness of semi-dry grasslands was largely governed by generalists also differs from that generally reported in the literature (Öster et al. 2007, Cachovanová et al. 2012). Again, different methods of identifying specialists may be the reason, as we considered only the specialists that occur in *Bromion erecti* and *Cirsio-Brachypodium pinnati* grasslands.

Cross-taxon comparison

The contrasting patterns recorded for vascular plant and bryophyte species richness along the moisture gradient could be explained in terms of competition between these two groups. As bryophytes can absorb nutrients directly from water through their whole surface, they can survive in nutrient-poor, but waterlogged fen habitats. Because vascular plants produce less biomass here bryophytes can cover up to 100% of the ground in these habitats. This is in accordance with the results recorded for Estonian species-rich dry calcareous grasslands, where bryophyte productivity is negatively associated with vascular plant productivity (Niinemets & Kull 2005). In addition, there is a strong overrepresentation of specialist bryophytes in fens, suggesting more intense environmental filtering in fens. This difference between vascular plants and bryophytes confirms the result of the large-scale study of Hájek et al. (2011). Although the pattern of species richness recorded along the moisture gradient differed for the taxonomic groups studied, Mantel tests revealed a highly significant correlations between all three abundance matrices (vascular plants, bryophytes and molluscs), which indicates similar rates of species turnover along the gradient studied.

In a previous study, species richness of molluscs was not correlated with the moisture gradient or any other environmental variable except for biomass weight (Hettenbergerová et al. 2013). This result corresponds more to that recorded for bryophytes than for vascular plants as overall bryophyte species richness was correlated only with moisture (but linearly so, in contrast to vascular plants). The reasons why the densities of bryophytes and molluscs species vary differently may include smaller body size associated with a dependence on small-scale structural properties such as microclimate or the shaded conditions that prevail under a vascular plant canopy, lack of large below ground organs, shorter life span and

greater mobility (Horsák et al. 2012). We found remarkable changes in species composition along the gradient for vascular plants, bryophytes and molluscs. First DCA axes of vascular plant, bryophyte (this study) and molluscan (Hettenbergerová et al. 2013) species data were long, which indicates the data is heterogeneous and there was a high species turnover along the moisture gradient.

Individual species performance along the moisture gradient

The most frequent species, i.e. the species with highest tolerance of the variability in moisture (Fig. 5), was *Carex flacca*. This species is often recorded not only in rich-fen grasslands (Hájková et al. 2004, Hájek et al. 2013) but also in various types of semi-dry grassland (e.g. Chytrý et al. 2007, Dúbravková et al. 2010, Škodová et al. 2011). Another common species with a wide moisture tolerance, *Calliergonella cuspidata* and *Briza media* are usually classified as either wetland or dry-grassland species, respectively (Chytrý 2011). Their wide tolerance of moisture recorded in this study is similar to that recorded by other studies carried out in the same region (Rozbrojová & Hájek 2008, Hájek et al. 2013). The importance placed on the diagnostic value of these species in the vegetation survey of the Czech Republic (Chytrý 2011) is therefore not valid at the scale of the calcareous areas in the Western Carpathian flysch zone.

The performances of the different local species recorded along the moisture gradient result in a unimodal species richness pattern for vascular plants, the organisms whose richness in the study area is exceptional globally (Wilson et al. 2012). Directly measured moisture levels were not included in the studies that attempted to account for the extremely high species richness of temperate grasslands. Our results suggest that further research on this topic should include detailed measurements of moisture.

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Souhrn

V této práci jsme se zaměřili na vlhkostní gradient vedoucí z prameništění vegetace do travinné. Pro studium jsme si vybrali vápnitou oblast Bílých Karpat a Vsetínské hornatiny na území České a Slovenské Republiky, kde se v komplexech široolistých suchých trávníků vyskytují malá pěnovecová prameniště. Na 15 lokalitách (transektech) jsme zapsali celkem 126 malých vegetačních snímků o velikosti 75 x 75 cm. Transekt vedl vždy z nejvlhčího místa prameniště přes jeho okraj do suchého trávníku. Pro stanovení množství živin (N, P, K, C, Ca) jsme odebírali vzorky půdy a biomasy a také jsme měřili vlhkost horní vrstvy půdy. Data byla vyhodnocena různými statistickými metodami včetně smíšených kvadratických modelů. Tento metodický postup nám umožnil přímo testovat čistý vliv vlhkosti na druhovou bohatost, bez výrazného ovlivnění rozdílů mezi lokalitami a jinými faktory prostředí. Počet druhů cévnatých rostlin vykazoval unimodální odpověď s optimem

posunutým do nižších hodnot vlhkosti. Tento výsledek však nebyl zapříčiněn jen vlivem okrajového efektu, neboť po nahrazení půdní vlhkosti standardizovanou pozicí plochy na transektu byla odpověď unimodální jen slabě. Dalším argumentem proti vysvětlení tohoto výsledku vlivem okrajového efektu je existence druhů, které upřednostňovaly spíše středně suchá a druhově bohatá místa, a zároveň se nevyskytovaly ani v prameništích ani v sušších loukách. Korelace mezi počtem druhů a produktivitou (pozitivní) a vápníkem v půdě (negativní) se lišily od většiny výsledků uváděných v literatuře, což ukazuje, že vztah mezi vlhkostí a druhovou bohatostí pravděpodobně nebyl v našem datovém souboru těmito faktory ovlivněn. V případě korelací s poměrem N:P v biomase, který indikuje úroveň limitace produktivity přístupností fosforu, jsme v souladu s jinými studiemi zjistili negativní vztah k celkovému počtu druhů a pozitivní vztah k zastoupení ohrožených druhů; vlhkost půdy však s těmito proměnnými korelovala silněji. Druhová bohatost mechorostů lineárně klesala směrem k suchým loukám a nekorelovala s žádnými dalšími měřenými prvky. Na prameništích tvořili druhovou bohatost cévnatých rostlin i mechorostů specialisti, zatímco velký počet druhů v sušších trávnících, včetně druhově nejbohatších ploch, byl tvořen spíše generalisty. V případě mechorostů stoupal podíl specialistů směrem do vlhka prudčeji než tomu bylo u cévnatých rostlin. Ačkoli změny druhového složení mechorostů a cévnatých rostlin podél vlhkostního gradientu spolu korelovaly (Mantelův test vyšel silně signifikantně), prokázali jsme značný rozdíl ve změnách druhové bohatosti. Domníváme se, že půdní vlhkost by měla být častěji brána do úvahy při vysvětlování diverzity temporární travinobylinné vegetace.

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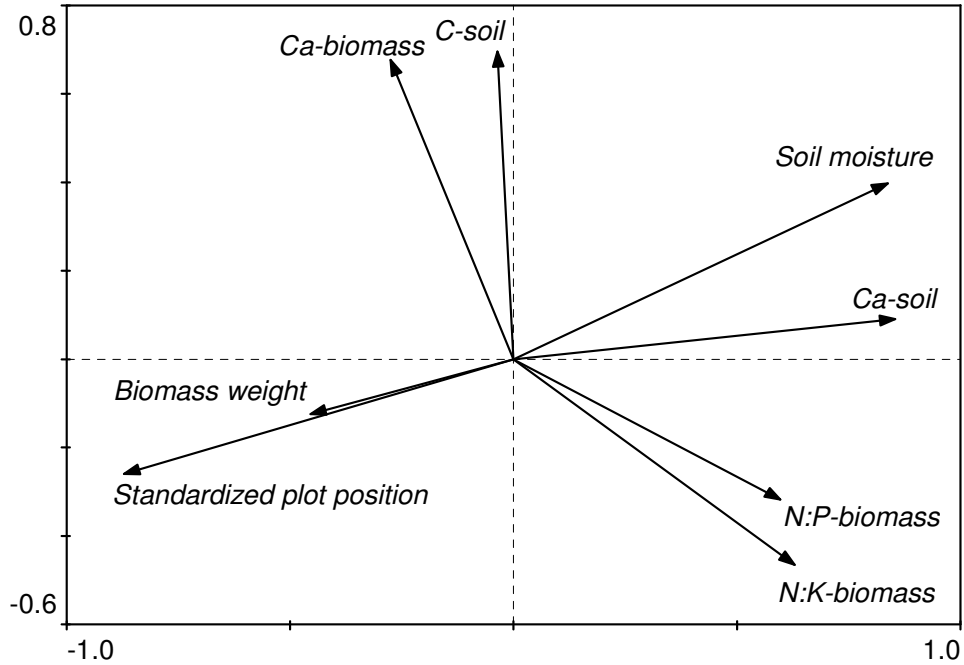
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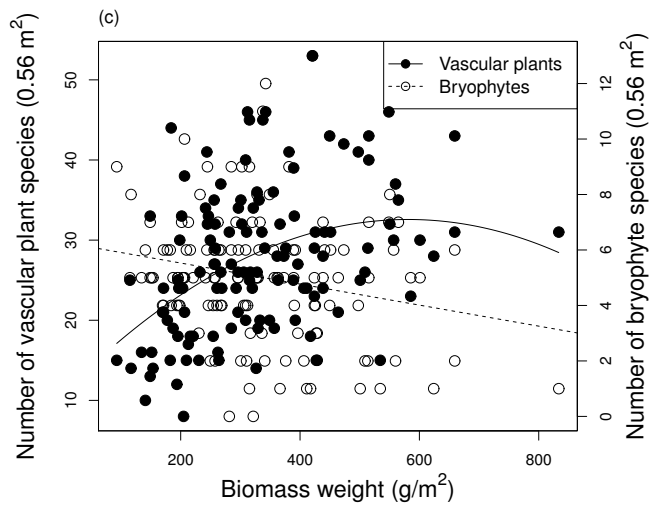
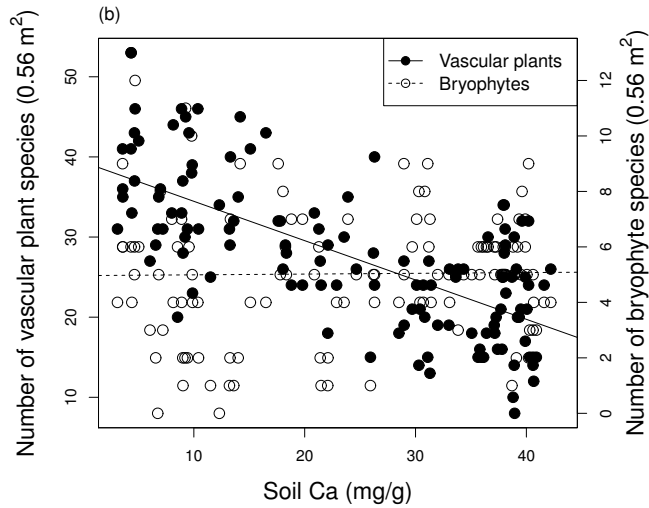
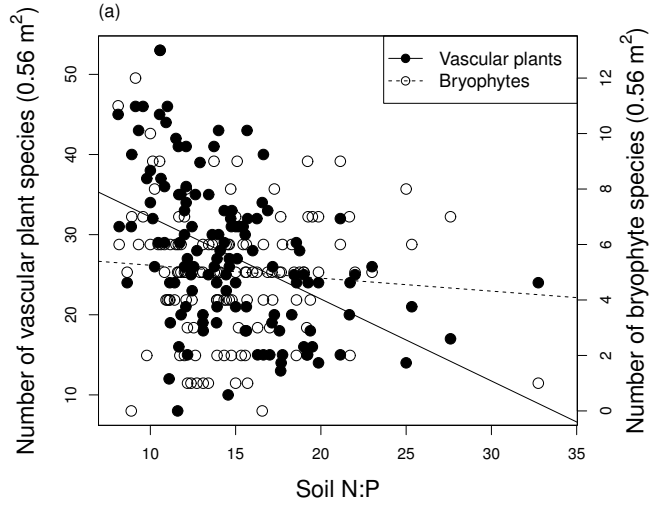
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Electronic Appendix 1. Descriptive statistic of all variables.

	Minimum	Lower quartile	Median	Mean	Upper quartile	Maximum	Standard deviation
Number of species							
Vascular plants	8	20	26.5	27.37	33	53	9.17
Bryophytes	0	4	5	5.032	6	13	2.37
Soil							
Moisture (%)	18.8	37.13	63.83	60.18	85.02	98.28	26.38
C (%)	3.32	8.47	10.05	11.7	14.34	30.36	5.11
Ca (mg/g)	3.1	10.4	26.3	24.4	37.6	42.2	13.03
Biomass							
Weight (g/m ²)	92.8	234.6	313.6	331.2	416.0	833.6	134.4
Ca (%)	0.35	0.69	0.855	0.916	1.068	1.97	0.3
N:P	8.11	11.79	14.04	14.72	16.97	32.75	4.12
N:K	0.45	0.61	0.695	0.713	0.78	1.3	0.14

Electronic Appendix 2. Principal component analysis (PCA) diagram of environmental data used in analyses.





Electronic Appendix 3. Relationship between species density of vascular plants and bryophytes and measured variables: N:P ratio (a), soil calcium (b) and vascular plant biomass weight (c). The regression for vascular plants in graph (c) was fitted by polynomial regression, another variables by linear regression.

Electronic Appendix 4. Abbreviations, full names and included species of taxons.

Abbreviation	Species name	Included species
Vascular plants		
Ace cam	Acer campestre	
Ace pse	Acer pseudoplatanus/platanoides	
Agr cap	Agrostis capillaris	
Agr eup	Agrimonia eupatoria	
Agr sto	Agrostis stolonifera	
Ach mil	Achillea millefolium agg.	A. collina, A. millefolium, A. pannonica, A. pratensis
Aju rep	Ajuga reptans	
Alc vul	Alchemilla vulgaris s.lat.	A. baltica, A. crinita, A. flabellata, A. glabra, A. glaucescens, A. micans, A. monticola, A. suavis, A. subcrenata, A. vulgaris, A. xanthochlora
All sco	Allium scorodoprasum	
Ant odo	Anthoxanthum odoratum	
Ant ram	Anthericum ramosum	
Aqu vul	Aquilegia vulgaris	
Arr ela	Arrhenatherum elatius	
Ave pub	Avenula pubescens	
Bet off	Betonica officinalis	
Bet pen	Betula pendula	
Bra pin	Brachypodium pinnatum	
Bri med	Briza media	
Bro ere	Bromus erectus	
Cal epi	Calamagrostis epigejos	
Cam glo	Campanula glomerata	
Car bet	Carpinus betulus	
Car car	Carex caryophyllea	
Car dav	Carex davalliana	
Car dis	Carex distans	
Car flac	Carex flacca	
Car flav	Carex flava	
Car hir	Carex hirta	
Car lep	Carex lepidocarpa	
Car mon	Carex montana	
Car nig	Carex nigra	
Car pal	Carex pallescens	
Car pane	Carex panicea	
Car panu	Carex paniculata	
Car tom	Carex tomentosa	
Cen jac	Centaurea jacea agg.	C. jacea, C. oxylepis
Cir arv	Cirsium arvense	
Cir can	Cirsium canum	
Cir ole	Cirsium oleraceum	
Cir pan	Cirsium pannonicum	
Cir riv	Cirsium rivulare	
Col aut	Colchicum autumnale	
Cra spe	Crataegus species	C. levigata agg., C. monogyna
Cre pal	Crepis paludosa	
Cru ver	Cruciata verna	
Dac glo	Dactylis glomerata	
Dac inc	Dactylorhiza incarnata	
Dac maj	Dactylorhiza majalis	
Dan dec	Danthonia decumbens	
Des ces	Deschampsia cespitosa	
Dor her	Dorycnium herbaceum	
Epi pal	Epipactis palustris	
Equ arv	Equisetum arvense	
Equ flu	Equisetum fluviatile	
Equ pal	Equisetum palustre	
Equ tel	Equisetum telmateia	
Eri ang	Eriophorum angustifolium	
Eri lat	Eriophorum latifolium	

Abbreviation	Species name	Included species
Eup can	<i>Eupatorium cannabinum</i>	
Eup cyp	<i>Euphorbia cyparissias</i>	
Fes pra	<i>Festuca pratensis</i>	
Fes rub	<i>Festuca rubra</i>	
Fes rup	<i>Festuca rupicola</i>	
Fil vul	<i>Filipendula vulgaris</i>	
Fra exc	<i>Fraxinus excelsior</i>	
Fra vir	<i>Fragaria viridis</i>	
Gal alb	<i>Galium album</i>	
Gal ver	<i>Galium verum</i>	
Ger pal	<i>Geranium palustre</i>	
Gle hed	<i>Glechoma hederacea</i>	
Hel gra	<i>Helianthemum grandiflorum</i> ssp. obscurum	
Hol lan	<i>Holcus lanatus</i>	
Hyp mac	<i>Hypericum maculatum</i>	
Hyp tet	<i>Hypericum tetrapterum</i>	
Inu sal	<i>Inula salicina</i>	
Jun art	<i>Juncus articulatus</i>	
Jun inf	<i>Juncus inflexus</i>	
Kna arv	<i>Knautia arvensis</i> agg.	<i>K. arvensis</i> , <i>K. kitaibelii</i>
Lat pra	<i>Lathyrus pratensis</i>	
Leo his	<i>Leontodon hispidus</i>	
Leu vul	<i>Leucanthemum vulgare</i> agg.	<i>L. ircutianum</i> , <i>L. margaritae</i> , <i>L. vulgare</i> subsp. <i>vulgare</i>
Lin cat	<i>Linum catharticum</i>	
Lot cor	<i>Lotus corniculatus</i>	
Lot mar	<i>Lotus maritimus</i>	
Luz cam	<i>Luzula campestris</i> agg.	<i>L. campestris</i> , <i>L. divulgata</i> , <i>L. multiflora</i>
Lyc eur	<i>Lycopus europaeus</i>	
Lys num	<i>Lysimachia nummularia</i>	
Lys vul	<i>Lysimachia vulgaris</i>	
Lyt sal	<i>Lythrum salicaria</i>	
Med lup	<i>Medicago lupulina</i>	
Men arv	<i>Mentha arvensis</i>	
Men lon	<i>Mentha longifolia</i>	
Mol aru	<i>Molinia arundinacea</i>	
Myo pal	<i>Myosotis palustris</i> agg.	<i>M. brevisetacea</i> , <i>M. nemorosa</i> , <i>M. palustris</i> subsp. <i>laxiflora</i>
Pim sax	<i>Pimpinella saxifraga</i> ssp. <i>saxifraga</i>	
Pin spe	<i>Pinus</i> species	<i>P. nigra</i> , <i>P. sylvestris</i>
Pla lan	<i>Plantago lanceolata</i>	
Pla med	<i>Plantago media</i>	
Poa pra	<i>Poa pratensis</i>	
Pol ama	<i>Polygala amarella</i>	
Pol cmv	<i>Polygala vulgaris</i> agg.	<i>P. comosa</i> , <i>P. multicaulis</i> , <i>P. vulgaris</i>
Pot ere	<i>Potentilla erecta</i>	
Pot hep	<i>Potentilla heptaphylla</i>	
Pot rep	<i>Potentilla reptans</i>	
Pri ver	<i>Primula veris</i>	
Pru spe	<i>Prunus</i> species	<i>P. avium</i> , <i>P. domestica</i> , <i>P. spinosa</i>
Pru vul	<i>Prunella vulgaris</i>	
Ran acr	<i>Ranunculus acris</i>	
Ran pol	<i>Ranunculus polyanthemos</i>	
Ran rep	<i>Ranunculus repens</i>	
Ros spe	<i>Rosa</i> species	<i>R. canina</i> , <i>R. dumalis</i> , <i>R. gallica</i>
Rum ace	<i>Rumex acetosa</i>	
Sal pra	<i>Salvia pratensis</i>	
San min	<i>Sanguisorba minor</i>	
San off	<i>Sanguisorba officinalis</i>	
Sci syl	<i>Scirpus sylvaticus</i>	
Sec var	<i>Securigera varia</i>	
Suc pra	<i>Succisa pratensis</i>	
Tar sec	<i>Taraxacum</i> sect. <i>Ruderalia</i>	

Vascular plants and bryophytes along moisture gradient.

Abbreviation	Species name	Included species
Teu cha	Teucrium chamaedrys	
Thy pul	Thymus pulegioides	
Tra ori	Tragopogon orientalis	
Tri fla	Trisetum flavescens	
Tri med	Trifolium medium	
Tri mon	Trifolium montanum	
Tri pal	Triglochin palustris	
Tri pra	Trifolium pratense	
Tus far	Tussilago farfara	
Val dio	Valeriana dioica	
Val off	Valeriana officinalis agg.	V. officinalis, V. stolonifera subsp. angustifolia
Ver cha	Veronica chamaedrys	
Vic cra	Vicia cracca	
Vic ten	Vicia tenuifolia	
Vio spe	Viola species	V. arvensis, V. canina, V. hirta, V. odorata, V. pumila, V. reichenbachiana, V. riviniana, V. suavis
Bryophytes		
Ane pin	Aneura pinguis	
Bra alb	Brachythecium albicans	
Bra riv	Brachythecium rivulare/rutabulum	
Bry pse	Bryum pseudotriquetrum	
Cal cus	Calliergonella cuspidata	
Cam ste	Campylium stellatum	
Cir pil	Cirriphyllum piliferum	
Cli den	Climacium dendroides	
Cra fil	Cratoneuron filicinum	
Cte mol	Ctenidium molluscum	
Fis adi	Fissidens adianthoides	
Fis dub	Fissidens dubius	
Fis tax	Fissidens taxifolius	
Hom lut	Homalothecium lutescens	
Oxy hia	Oxyrrhynchium hians	
Pal com	Palustriella commutata	
Phi cal	Philonotis calcarea	
Pla aff	Plagiomnium affine agg.	P. affine, P. elatum, P. ellipticum, P. medium
Pla und	Plagiomnium undulatum	
Pse pur	Pseudoscleropodium purum	
Rhy tri	Rhytidiadelphus triquetrus	
Thu ass	Thuidium assimile	
Wei spe	Weissia species	W. brachycarpa, W. controversa, W. longifolia, W. rostellata, W. rutilans, W. squarrosa

Testing community assembly predictions for nominal and continuous plant traits in species-rich grasslands

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Dedicated to the memory of Leoš Klimeš

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Abstract

We investigated patterns of trait-based community assembly in grasslands sampled along a moisture gradient (216 species) using three continuous species-level traits (maximum species height, minimum species height, seed mass), as well as seven nominal traits (flowering phenology, fruit type, pollen vector, clonal growth organs – CGOs, branching type, leaf distribution, lateral spread), some of which are unusual in that a species may possess more than one state per trait simultaneously (e.g. CGO). Additionally, this study tests whether patterns of assembly vary with plot biomass and moisture using both presence-absence and abundance-weighted analyses (two plot sizes: 25 × 25 cm, 75 × 75 cm). Plant species in these grasslands were randomly organized with respect to both maximum and minimum species height; however, coexisting plant species had a significantly smaller mean seed mass than expected by chance, and were significantly convergent in seed mass, consistent with observations from one previous study, and with theory related to environmental or competitive filtering. These patterns were consistent across plot sizes, and were similar whether analyses were abundance-weighted or not, although partitioned analyses show that these patterns are most pronounced in wet grasslands. Grasslands were non-randomly assembled with respect to five of our ten traits including seed mass, fruit type, CGO, branching type and leaf distribution. Among these, only patterns of branching type clearly conformed to the predictions from Limiting Similarity Theory, suggesting that variation in this trait may contribute to species coexistence in these grasslands. In two cases (fruit type, branching type), results differed in significance depending on whether analysis used presence-absence or abundance data; incorporating abundance may be more relevant, however, cover-based abundance measures in small plots can bias trait representation in favour of size over ramet number. In general, patterns were consistent across the two plot sizes. For four traits (seed mass, flowering phenology, leaf distribution and lateral spread) plot-level effect sizes of our tests varied significantly with plot-level biomass production; the slope of these relationships was positive for seed mass, but negative for flowering phenology, leaf distribution and lateral spread. For seven of ten traits, plot-level effect sizes varied significantly with plot-level soil moisture, with positive regression slopes for some traits (flowering phenology, leaf distribution), and negative slopes for others (minimum height, seed mass, fruit type, pollen vector, CGO). These results indicate that community assembly rules related to different functional traits can be responsive to variation in either biomass or soil moisture, or both.

Key words: coexistence, diversity, environmental filtering, functional diversity, limiting similarity, plant functional traits, trait convergence, trait dispersion, trait divergence

Introduction

An increased interest in functional diversity, perhaps a more ecologically meaningful subset of taxonomic diversity (McGill et al. 2006, Messier et al. 2010, Webb et al. 2010), has emerged within the field of ecology, placing a greater emphasis on studies exploring the importance of variation in species-level traits in driving deterministic patterns of community assembly (e.g. Weiher et al. 1998, Weiher & Keddy 1999, Franzén 2004, Stubbs & Wilson 2004, Mouillot et al. 2005b, Grime 2006, Schamp et al. 2008, 2010, Schamp & Aarssen 2009). Coincident with this focus on functional variation has been the development and refinement of theories related to trait-based community assembly (e.g. Weiher & Keddy 1995, Weiher et al. 1999, Grime 2006, Wilson 2007), as well as a renewed interest in testing predictions that coexisting species should differ with respect to traits related to resource requirement (i.e. Limiting Similarity Theory; MacArthur & Levins 1967).

While progress has been made, advancement has been limited by available trait data, and perhaps by the limited availability of programs/algorithms for the appropriate null models that have emerged as standard for testing predictions related to trait over- and underdispersion (trait convergence/divergence, trait spread or clustering) (Weiher et al. 1998, Stubbs & Wilson 2004, Mouillot et al. 2005a, Schamp et al. 2008, 2010, de Bello et al. 2009, Schamp & Aarssen 2009). Consequently, a great deal more work is required to explore the consistent contribution of functional traits to community assembly; four challenges exist within the framework of this field. First, evidence thus far, although limited, suggests that patterns of trait-based assembly are scale-dependent (Stubbs & Wilson 2004, Schamp et al. 2008, Messier et al. 2010); most studies thus far have focused on a single scale of analysis (e.g. Weiher et al. 1998, Franzén 2004, Schamp & Aarssen 2009). Further studies are needed that assess the influence of particular traits across scales both within and among communities. Second, a limited number of traits have been considered, most of which have been chosen largely for convenience, rather for their potential importance in community assembly (but see Stubbs & Wilson 2004). However, selecting recognized functional traits is perhaps only one available solution to this problem. The current approach, which has focused on species-level traits that are readily available either in the literature, or in databases, is beneficial because it allows researchers to explore the potential influence of species-level traits that have been hitherto unexplored in the area of community ecology. This approach should be extended, albeit with care to avoid problems with multiple tests, to also explore possible correlations between traits being examined, as a way of more clearly assessing which traits are driving patterns. One approach would be to collapse many continuous traits into a few ordination axes. Third, few studies have explored these patterns using nominal traits (but see Stubbs & Wilson 2004, Schamp et al. 2010). Such studies should be expanded, to enable researchers to both (i) address current theoretical predictions regarding trait dispersion, and (ii) use existing null model tests to objectively determine which traits can accurately be described as “functional traits”. Fourth, several studies have found contrasting results related to the dispersion of plant species traits. For example, Franzén (2004) observed that seed mass was significantly underdispersed within a grassland community. This contrasts with a study by Schamp et al. (2008) in which species in an old-field plant community were neither significantly over- or underdispersed with respect to this trait. Similarly, Weiher et al. (1998) found evidence that maximum species height was overdispersed among wetland plots, while Schamp et al. (2008) and Schamp & Aarssen (2009) found no significant pattern for this trait in an old-field community, and among forest communities, respectively. These limited results suggest that patterns may be both scale- and community/habitat specific, with differences in findings possibly linked to a number of factors. Several approaches may be used to address these challenges. Large-scale studies examining many different functional traits will come with time, and will play an important role. In the meantime, immediate progress can be made through multiple studies targeting

different communities, and a variety of functional trait data. While this is a problem, it is also clear that the approach taken has yielded interesting results, and has accomplished a great deal in the development of statistical techniques for assessing deterministic trait-based community assembly (e.g. Weiher et al. 1998, Franzén 2004, Stubbs & Wilson 2004, Schamp et al. 2010).

Furthermore, what may appear to be confusingly diverse patterns among the small number of studies that have been done, may yet reveal consistency when additional consideration is given to such issues as scale of analysis (also plot size), the relative contribution of non-native species to communities, and successional stage. This work will be aided by the growing number of trait databases becoming available, e.g. LEDA Traitbase (Kleyer et al. 2008) or CLO-PLA database (Klimešová & Klimeš 2006, 2008, Klimešová & de Bello 2009), as well as the proliferation of public databases connecting researchers with community data that may be combined for more comprehensive analyses (e.g. connection with large vegetation-plot databases; Schaminée et al. 2009). A larger number of studies exploring these patterns are required to test predictions related to the general influence of particular traits on plant community assembly.

This study sets out to address several of the issues surrounding research exploring the influence of important species-level traits on community dynamics. We use a large data set consisting of paired plots (two plot sizes) sampled along the existing moisture gradient in species-rich grasslands and a collection of 10 species-level traits, to test the following questions: (i) Are the chosen species-level traits, several of which have been highlighted as playing important roles in vegetation processes (e.g. plant height in competition and invasion: Gaudet & Keddy 1988 and Schamp & Aarssen 2010, respectively; CGOs in local dispersal: Klimeš 2008, Klimešová & Klimeš 2008), significant drivers of non-random species organization in a species-rich grassland? (ii) Are predictions related to Limiting Similarity Theory more generally supported in a species-rich grassland community, where potential for overlap in resource requirements among species may be expected to increase the instances of interspecific competition? (iii) Do observed patterns differ for different plot sizes and when presence-absence vs abundance data is used? (iv) Do assembly patterns vary across gradients of plot-level biomass production and soil moisture, as expected if these gradients are related to environmental stress (Weiher & Keddy 1995), and consistent with patterns observed for some species-level traits in other studies (Schamp et al. 2008, 2010)?

Materials and methods

Study sites

All study localities are situated in Central Europe in Western Carpathian Mountains on the southern part of the border between Czech and Slovak Republic, with most localities in the Bílé Karpaty Mountains. This area is formed by flysh – the bedrock is composed of alternating claystones and sandstones. The annual mean precipitation is approximately 700 mm and the annual mean temperature is about 8 °C (Miklós 2002, Tolasz 2007). The altitude of localities varies between 270 and 550 m a.s.l. (average 442 m). The grasslands in the study area are floristically unique (Hájková et al. 2011).

The study system is a mosaic of small (several square metres) spring calcareous fen sedge-moss wet grasslands scattered within herb-rich semi-dry grasslands. The soil moisture varied from 98% in wet plots to 19% in plots located in neighbouring semi-dry grasslands. Fen vegetation consists mostly of small sedges and non-sphagnaceous mosses, as well as a variety of grasses and herbs (the *Caricion davallianae* alliance, cf. Hájek et al. 2006), while semi-dry grassland vegetation is characterized primarily by grasses, herbs and sedges and is classified within *Festuco-Brometea* class (alliance *Cirsio-Brachypodium pinnati* and *Bromion*

erecti). Fen-grassland transitions are sometimes formed by vegetation dominated by herbs, grasses, taller sedges and rushes, classified within *Calthion* alliance.

Field sampling

All field data were collected between June and July during the years 2005–2008. Data collection always consisted of establishing one linear transect (8–30 m) extending from the wettest part of spring fen grassland to dry grassland on 15 localities. The number of plots recorded per fen (5 to 16 plots) depended on size of the spring fen grassland; data from 126 plots (of the size 75 × 75 cm) were recorded. The exact distance between the centres of neighbouring plots was 2 metres. Within each larger plot (75 × 75 cm), a smaller, nested sample (25 × 25 cm) was recorded and standing plant biomass was collected. In each plot, species cover was estimated using a nine-grade scale (van der Maarel 1979). Biomass was subsequently dried at 60 °C for several days and weighted. Soil moisture in the upper most soil horizon was measured for each 25 × 25 cm plot during the driest period of the year (July to September; ThetaProbe, soil moisture sensor ML2x).

The nomenclature of plant species follows Kubát et al. (2002), syntaxonomical nomenclature is according to Chytrý (2007).

Species-level plant traits

Species-level plant traits (Electronic Appendix 1) were obtained from multiple sources: (i) Czech flora (Kubát et al. 2002): maximum and minimum species height; (ii) BioFlor database: flowering phenology, fruit type, pollen vector (Klotz et al. 2002); (iii) CLO-PLA database: clonal growth organs (CGOs), branching type, leaf distribution, lateral spread (Klimešová & Klimeš 2006, 2008, Klimešová & de Bello 2009). Seed mass data were taken from the Ecological Flora of the British Isles online database (Fitter & Peat 1994), from the Seed Information Database (Royal Botanic Gardens Kew 2008) and from Moles et al. (2005). Additional seed mass data were obtained for nine additional species by weighing between 30–100 seeds per species (depending on availability) from samples in the Seed and Fruit Collection of the Institute of Botany of the ASCR (<http://www.ibot.cas.cz>).

Some trait data were not available for some species. Missing trait data were dealt with in two ways: (i) by calculating the average proportion of species in plots that were missing data for each trait; (ii) the use of sensitivity tests to test whether the results of our tests differed when a subset of plots consisting of less missing trait data were analyzed (see below). For presence-absence data, the proportion of missing trait data was measured as the number of species per plot with missing trait data divided by the total number of species in that plot. For abundance analyses, the proportion of missing trait data was calculated as the abundance of species in a plot with missing trait data divided by the total abundance of plants in that plot. In general, missing data made up only a small proportion of the species in plots (Electronic Appendix 2); flowering phenology contained the highest proportion of missing data, and consequently was used in the aforementioned sensitivity analysis.

Analysis: continuous and nominal plant traits

We used an established null model to test for deterministic (i.e. non-random) organization of plant species according to three continuous plant traits: maximum height, minimum height (presumably observed at reproductive maturity) and seed mass. We tested for trait advantages using a test statistic developed by Schamp & Aarssen (2009; mean trait value) and tested for evidence of either over- or underdispersion (also divergence vs convergence; trait spread vs clumping) using previously developed test statistics (Stubbs & Wilson 2004, Schamp et al. 2008, Schamp & Aarssen 2009). Patterns related to trait overdispersion/divergence/spread support theoretical predictions under Limiting Similarity Theory (MacArthur & Levins 1967), and patterns of underdispersion support theoretical predictions of trait convergence due to competitive filtering (Grime 2006), or environmental

filtering (Weiher & Keddy 1995). This analysis compares different measures of trait distributions to a distribution of the same measures generated by randomly assigning traits among all species in the community (i.e. null distribution; Schamp et al. 2008, 2010, Schamp & Aarssen 2009). Distributions of each community-level test statistic were generated from 5000 randomizations of the trait matrix. All null model tests are two-tailed tests, with P-values calculated as: $P = \text{MIN} [2S/(3001), 2L/(3001)]$ with S and L equal to the number of randomized test statistics greater than or equal to, or less than or equal to the measured test statistic respectively (cf. Bersier & Sugihara 1997, see also Schamp et al. 2008, Schamp & Aarssen 2009). All analyses were carried out in Matlab® using code developed by Schamp. Separate analyses were conducted using presence-absence data as well as abundance data; these two approaches can produce different results (e.g. Schamp et al. 2008).

We used several test statistics (trait distribution measures), all of which have previously been used in similar analyses (e.g. Stubbs & Wilson 2004, Schamp et al. 2008). In each case, the statistic is calculated for each plot and trait, and the mean of all plot-level values (i.e. community mean) is used as the test statistic. These include: (i) Mean – This measure was used to assess whether one end of a given trait distribution is favoured or not (Schamp & Aarssen 2009). If coexisting plants have a greater maximum height than expected, for example, this may be interpreted as evidence that tall plants are favoured. (ii) Range – This measure is the maximum trait value minus the minimum trait value for a particular plot. When this test statistic is larger than expected by chance, this can be taken as evidence for Limiting Similarity Theory, and if it is smaller than expected, it is accepted as evidence of significant trait convergence. (iii) Mean Nearest Trait Distance (meanNTD) – This was calculated for each plot by ordering species from smallest to largest for each trait, and determining the mean difference in trait value (Euclidean) between each species and its closest neighbour. The mean of plot-level meanNTD among all plots was used as the measure of how spaced species are with respect to traits, within plots. Higher meanNTD values than expected support Limiting Similarity Theory (Weiher & Keddy 1995), and smaller meanNTD values suggest trait convergence (Grime 2006). (iv) Variance in Nearest Trait Distance (varNTD) – This is the variance in those distances among coexisting species described for meanNTD; this is a measure of how regularly spaced coexisting species are with respect to each trait. Values of varNTD that are lower than expected have been cited as support for Limiting Similarity Theory (Stubbs & Wilson 2004). (v) Richness – This test statistic was used for nominal/categorical traits and is a measure of the number of categories represented within a sample. If richness is higher than expected by chance, this would suggest evidence of limiting similarity, and a lower than expected value of richness would indicate that some trait categories are favoured over others. This measure is less useful for traits with few categories, as possible variation in richness among plots tends to be low, or in some cases non-existent. (vi) Evenness – This statistic was also used with categorical data and is a measure of how evenly represented different categories were within samples. This measure addresses concerns that functional diversity should be measured both in terms of richness and evenness (Mason et al. 2005, Mouillot et al. 2005a). High evenness is taken here as evidence in support of Limiting Similarity Theory, while lower evenness than expected would indicate some categories are more favoured. For traits with few categories, high evenness may also result if species richness is lower than expected; this is because a plot represented by a single category for a trait would be measured as maximally even. We discuss these issues in the results as they arise.

Analysis: nominal traits for which a species may possess multiple states

Some potentially informative categorical traits pose problems for analysis because categories for that trait may not be mutually exclusive, meaning that some species may have multiple trait-states for a given categorical trait. A given species, for example, may possess several different CGOs at the same time, so for this particular trait, that species has multiple

values. To handle this, the same model was employed as described above; however, distributions of traits for plots were composed of all trait-states represented, so for presence-absence data, the number of trait-states for a given plot was equal to the number of trait values exhibited by the species in that plot. In general, the trait distribution contained more values than there were species in that plot. If a given species possessed three different CGOs, this was represented in plots by all three trait-states, contributing the same level of trait variation as would three different species with one CGO each. Similarly, for abundance analyses with such traits, the number of trait-states in a given plot was generally higher than the total plant abundance for that plot. In the current analysis, it is therefore assumed that each species displays all possible states for such traits, in each plot. This may be unreasonable, and we recommend that future studies actually measure what states are displayed for each of these traits in each plot. As with other nominal traits, the same two test statistics were calculated (richness, evenness).

Sensitivity analysis

To test whether missing trait data may have impacted our results, we re-ran our tests for flowering phenology, the trait with the highest proportion of missing data (4.6% missing per plot for presence-absence data; 5.5% missing per plot for abundance data; Electronic Appendix 2). These tests included only plots for which all species-level flowering phenology data were available ($n = 68$ plots for 25×25 cm plots; 38 plots for 75×75 cm plots).

Community assembly along gradients

For one plot size (25×25 cm plots) we tested whether the plot-level effect sizes of our tests were responsive to plot-level variation in productivity and soil moisture by using regressions to test for directional changes in effect sizes (z-scores) of our tests among 25×25 cm plots (biomass was not collected for 75×75 cm plots). Z-scores for each plot and each test statistic were calculated as $(O-M)/S$, where O is the observed value for each test statistic and plot, and M and S are the mean and standard deviation respectively for each test statistic across 5000 randomizations of the trait distribution for the study plots (Schamp & Aarssen 2009, Schamp et al. 2010).

Analysis of wet and dry grasslands separately

Because it is possible that investigations of limiting similarity across gradients may bias results against supporting limiting similarity, which may likely be most strongly expressed in more homogeneous conditions, we also analyzed wet and dry grassland plots separately (wet grasslands: 52 plots; dry grasslands: 51 plots), excluding plots that were of intermediate moisture.

Results

Continuous plant traits

Species coexisting in our study plots were randomly organized with respect to maximum and minimum species height (Table 1). Additionally, our results indicate that coexisting species have significantly smaller seed masses than expected by chance (25×25 cm: $P = 0.0092$; 75×75 cm: $P = 0.00016$), and that seed size is significantly convergent in 25×25 cm plots (range: $P = 0.0084$; meanNTD: $P = 0.0056$; varNTD: $P = 0.0016$) and in 75×75 cm plots (range: $P = 0.00012$; meanNTD: $P = 0.0012$; varNTD: $P = 0.0148$). These patterns are reported for presence-absence analyses; however, in general, abundance-based analyses produced similar results, excepting results for meanNTD and varNTD, which generally do not produce significant results for abundance data because of the heavy weight placed upon these values by abundant species, the nearest neighbour of which will always be conspecifics with the same trait value.

Table 1. Results from trait dispersion analysis on three continuous species-level traits: maximum height, minimum height (minimum size at reproduction), and seed mass. Analyses used presence-absence and abundance data from 126 plots for each of two plot sizes (25 × 25cm, 75 × 75cm). P-values indicate whether plots are overdispersed (Obs > Exp), or underdispersed (Obs < Exp) for the trait of interest. Bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

	Test statistic	Presence-absence				Abundance			
		Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp	
		25×25	75×75	25×25	75×75	25×25	75×75	25×25	75×75
Maximum height	Mean			0.376	0.522			0.428	0.652
	Range			0.421	0.438			0.416	0.441
	Mean NTD			0.813	0.741			0.506	0.673
	Var NTD			0.438	0.092			0.291	0.273
Minimum height	Mean			0.266	0.251	0.603	0.527		
	Range			0.704	0.523			0.968	0.791
	Mean NTD			0.908	0.639			0.855	0.148
	Var NTD			0.436	0.056			0.537	0.062
Seed mass	Mean			0.009	<0.001			0.011	0.004
	Range			0.008	<0.001			0.004	0.003
	Mean NTD			0.006	0.001	0.958		0.661	
	Var NTD			0.002	0.015			0.414	0.918

Nominal plant traits

Because seven traits were examined at two scales and using two test statistics as well as both presence-absence and abundance data, we confine our written report to significant results, and refer readers to Table 2, which summarizes the results from all analyses.

In 25 × 25 cm plots, coexisting species were also non-randomly organized with respect to several nominal plant traits. In these small study plots, several traits were significantly less evenly distributed among coexisting species, indicating that some trait-states are favoured in plots (fruit type: $P = 0.0088$; CGOs: $P = 0.0028$; branching type: $P = 0.0336$). Each of these patterns was accentuated when analyses were weighted by abundance.

Also in 25 × 25 cm plots, coexisting species were observed to be more even than expected by chance with respect to leaf distribution ($P = 0.0012$); however, plots were also significantly less rich with respect to this trait ($P = 0.02$), indicating that low richness in this trait may have resulted in higher evenness (Table 2).

In 75 × 75 cm plots, similar patterns were observed, with coexisting species being less even than expected by chance with respect to two categorical traits (CGOs: $P = 0.0104$; branching type: $P = 0.0468$); significance of these results were higher when weighted by abundance (Table 2). Coexisting species in these plots were also less even than expected in regard to fruit type; however, this result was only significant for the abundance-weighted analysis ($P = 0.0212$). At this plot size, coexisting species were also possessed of a significantly richer number of branching types than expected by chance, a result expected under Limiting Similarity Theory ($P = 0.0416$).

Sensitivity test results

When flowering phenology analyses were run only using plot data for which all trait data were known (0% missing trait data/plot), coexisting species were randomly organized with respect to flowering time (Electronic Appendix 3). This finding is no different from that observed when the entire data set was analyzed; no further interpretation of these results was pursued.

Table 2. Results from trait dispersion analysis on seven nominal traits. P-values indicate whether plots are richer (Richness: Obs > Exp), or poorer (Richness: Obs < Exp) in terms of variation in these traits, and whether these traits are more evenly (Evenness: Obs > Exp), or less evenly (Evenness: Obs < Exp) distributed within plots. Studied traits include flowering phenology (month of flowering), fruit type, pollen vector, leaf distribution, clonal growth organ and branching type. The last four of these traits are unique in that a single species can have multiple values; for example, a species may be both insect and wind pollinated. This was incorporated into the analysis. Bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

	Test statistic	Presence-absence				Abundance			
		Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp	
		25×25	75×75	25×25	75×75	25×25	75×75	25×25	75×75
Flowering phenology	Richness		0.730	0.994		0.993	0.722		
	Evenness	0.125	0.870			0.087	0.852		
Fruit type	Richness			0.301	0.508			0.296	0.455
	Evenness			0.009	0.090			0.001	0.021
Pollen vectors	Richness		0.244	0.777		0.699	0.7028		
	Evenness	0.713			0.663			0.555	0.124
Clonal growth organ	Richness			0.416	0.838		0.678	0.879	
	Evenness			0.003	0.010			0.001	0.002
Branching type	Richness	0.058	0.042			0.774	0.647		
	Evenness			0.034	0.047			0.511	0.178
Leaf distribution	Richness			0.020	0.002			0.082	0.006
	Evenness	0.001	0.006			0.001	0.001		
Lateral spread	Richness			0.689	0.689			0.694	0.689
	Evenness			0.710	0.710			0.709	0.573

Community assembly along gradients

For 25 × 25 cm plots, patterns of organization in relation to traits were generally poorly responsive to plot level biomass (Tables 3–4). However, the tendency for coexisting plant species to be of smaller mean seed mass in plots was significantly higher in plots with high biomass ($P = 0.048$; Table 3), the opposite of the pattern expected if assembly rules for this trait are driven by environmental stresses (Weiher & Keddy 1995, Weiher et al. 1998). Among nominal traits, coexisting species tended to be less rich in flowering phenologies in plots with high biomass. This pattern was also observed for leaf distribution, and for lateral spread (Table 4). Coincident with the tendency for coexisting species to be less rich in leaf distribution in plots with high biomass, species were also less even in the distribution of different lateral spread strategies ($P = 0.002$).

Patterns varied significantly along the moisture gradient in this study for seven of ten traits (minimum height, seed mass, flowering phenology, fruit type, pollen vector, CGO and leaf distribution; Table 4). Plot-level effect sizes increased significantly with plot-level soil moisture for flowering phenology and leaf distribution, and decreased significantly for minimum height, seed mass, fruit type, pollen vector, CGOs. Importantly, slopes of these relationships were extremely close to zero and for most traits (but see flowering phenology) explained only a very small portion of the variance in observed effect sizes.

Analysis of wet and dry grasslands separately

When wet and dry grasslands were considered separately, which was done to ensure that patterns reflecting limiting similarity were not obscured by the inclusion of plots along the moisture gradient, no new evidence of overdispersion for our traits was uncovered either in wet (Electronic Appendix 4, 6), or dry (Electronic Appendix 5, 7) grasslands. However, in dry grasslands, significant underdispersion observed for seed mass in the larger analysis was no longer apparent (Electronic Appendix 4), although it remained for wet grasslands (Electronic Appendix 5). Significant underdispersion observed in the larger analysis was also removed in dry grasslands for fruit type, CGO and branching type (Electronic Appendix 6), although this change varied depending on plot size and the use of abundance-weighting in analyses. In dry grasslands, branching types were significantly more evenly represented in 25 × 25 cm plots than expected by chance; however, significance was marginal and would be erased by any effort to protect for multiple tests ($P = 0.046$; Electronic Appendix 6).

Table 3. Results from regression analyses testing whether plot-level effect sizes of our tests for each continuous trait and each test statistic change predictably with aboveground dry biomass production, and moisture of plots (25 × 25 cm plots). All regressions have a sample size of 126 plots; bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

Plot characteristic	Trait	Test statistic	Slope	R ²	P-value
Plot biomass	Maximum height	Mean	0.011	0.020	0.114
		Range	0.005	0.005	0.435
		Mean NTD	0.006	0.008	0.327
		Var NTD	0.005	0.012	0.230
	Minimum height	Mean	0.006	0.006	0.378
		Range	0.004	0.004	0.460
		Mean NTD	0.005	0.008	0.332
		Var NTD	0.005	0.013	0.202
	Seed mass	Mean	0.012	0.031	0.048
		Range	0.004	0.007	0.348
		Mean NTD	0.003	0.004	0.480
		Var NTD	0.019	0.004	0.127
Plot moisture	Maximum height	Mean	-0.003	0.021	0.108
		Range	0.001	0.002	0.611
		Mean NTD	0.002	0.006	0.409
		Var NTD	0.002	0.025	0.080
	Minimum height	Mean	-0.005	0.050	0.012
		Range	-0.001	0.001	0.762
		Mean NTD	-0.0004	0.001	0.811
		Var NTD	0.001	0.010	0.266
	Seed mass	Mean	-0.010	0.211	<0.001
		Range	-0.005	0.093	<0.001
		Mean NTD	-0.004	0.075	0.002
		Var NTD	0.0002	0.001	0.767

Table 4. Results from regression analyses testing whether plot-level effect sizes of our tests for each nominal trait and each test statistic change predictably with aboveground dry biomass production of plots (25 × 25 cm plots). All regressions have a sample size of 126 plots; bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

Plot characteristic	Trait	Test statistic	Slope	R ²	P-value
Plot biomass	Flowering phenology	Richness	-0.024	0.047	0.015
		Evenness	-0.004	0.001	0.722
	Fruit type	Richness	0.017	0.029	0.058
		Evenness	0.016	0.018	0.133
	Pollen vectors	Richness	0.020	0.024	0.082
		Evenness	-0.012	0.015	0.177
	Clonal growth organs	Richness	0.010	0.013	0.199
		Evenness	0.017	0.017	0.152
	Branching type	Richness	0.006	0.002	0.672
		Evenness	-0.011	0.014	0.181
	Leaf distribution	Richness	-0.027	0.095	< 0.001
		Evenness	-0.021	0.072	0.002
	Lateral spread	Richness	-0.025	0.035	0.035
		Evenness	-0.013	0.014	0.182
Plot moisture	Flowering phenology	Richness	0.019	0.285	<0.001
		Evenness	0.003	0.006	0.394
	Fruit type	Richness	-0.007	0.043	0.019
		Evenness	-0.009	0.058	0.007
	Pollen vectors	Richness	-0.009	0.045	0.017
		Evenness	-0.002	0.006	0.408
	Clonal growth organs	Richness	-0.001	<0.001	0.817
		Evenness	-0.020	0.202	<0.001
	Branching type	Richness	0.008	0.023	0.090
		Evenness	-0.001	0.002	0.655
	Leaf distribution	Richness	0.007	0.068	0.003
		Evenness	0.004	0.021	0.103
	Lateral spread	Richness	0.003	0.006	0.377
		Evenness	0.005	0.019	0.123

Discussion

Deterministic assembly of grassland communities

Our results indicate that plant species within this grassland mosaic are organized deterministically into plots of two different sizes, with respect to several plant traits. Significant patterns of either under- or overdispersion, or favoured trait-states were observed for five of the ten traits examined (Table 1). This finding supports the logic of a swelling interest in the impact of functional trait variation on patterns of plant community assembly (e.g. Weiher & Keddy 1995, Grime 2006, McGill et al. 2006, Wilson 2007). Additionally, our findings support the assertion (Schamp et al. 2010) that hitherto unrecognized functional plant traits can be discovered through the use of these models (e.g. fruit type, CGOs, branching types, lateral spread; Table 2).

Observed patterns reflected predictions from Limiting Similarity Theory for branching type in our larger plot size, with coexisting species being significantly richer in classes of this trait than expected by chance (Table 2). Additionally, branching types were less evenly distributed among coexisting species in these plots than expected by chance, such that richness was higher, but evenness was lower. Thus, in terms of richness, predictions from Limiting Similarity Theory are supported, but in terms of evenness, they are not. Regardless, this can be viewed as supporting evidence that different branching types may contribute to

coexistence via limiting similarity in these grasslands. Contrastingly, leaf distribution classes were significantly more evenly represented among coexisting species for both plot sizes; however, in both cases, coexisting species were significantly less rich in leaf distribution class than expected. In these cases, many plots were represented by only a single leaf distribution class, and therefore are significantly more even than expected by virtue of low richness. These findings illustrate the complexities of recognizing evidence of limiting similarity for nominal plant traits. The latter problem is less likely for nominal traits for which there are many different states (e.g. leaf distribution: 3 states vs CGO: 17 states). Care should be taken in interpreting this type of result as conclusive evidence supporting Limiting Similarity Theory.

Our results provide evidence of significant underdispersion (i.e. convergence) of several traits, in support of predictions by Grime (2006) that traits related to competition will be convergent as dominant trait states outcompete less competitive states. Additionally, these results are consistent with predictions from Weiher & Keddy (1995) that traits related to environmental tolerance will be convergent. Coexisting species possessed a smaller mean seed mass than expected by chance, and were significantly underdispersed for this trait at both plot sizes; these patterns were generally supported independent of whether presence-absence or abundance data were used (Table 1). This result is consistent with patterns observed by Franzén (2004) in a grassland community, but contrasts with patterns observed by Schamp et al. (2008) in an old-field community. Further testing should be conducted to determine whether dispersion patterns related to seed mass vary across a successional gradient. These patterns held in wet grasslands when these were considered separately (Electronic Appendix 5), but were not as prominent in dry grasslands (Electronic Appendix 4). This is further evidence that trait-based filtering of species will be accentuated in some environmental conditions (Weiher & Keddy 1995). Additionally, a number of nominal traits were less evenly distributed among coexisting species than expected by chance, which suggests that some nominal traits are favoured over others. Fruit type, CGOs and branching type were traits following this pattern (Table 2). These patterns were consistently observed for both plot sizes, with the exception that fruit type underdispersion was only significant at $\alpha = 0.05$ when analyses were weighted by abundance. These findings indicate that these traits are important for community assembly, and that particular trait states are favoured within communities.

Presence-absence vs abundance analyses

In a previous study, Schamp et al. (2008) observed that although significance of patterns did not differ between analyses using abundance vs presence-absence data, in some cases patterns that tended towards overdispersion for one type of analysis tended towards underdispersion when the other type of analysis was employed, suggesting that the choice of which analysis type to use may be important. Our results take this suggestion further by demonstrating that the use of these different analyses can lead to differences in the significance of observed results. For example, coexisting species for both plot sizes were significantly convergent in seed mass for all four test statistics employed when presence-absence data were used in analyses; however, when abundance data were examined, the spacing among individuals in seed mass was not significantly lower than expected (meanNTD; Table 1), nor less variable than expected (varNTD; Table 1). Part of this difference comes from the fact that in abundance analyses, individual plants count as individuals but still contribute species-level traits such that variation in both meanNTD and varNTD are driven primarily by the randomization procedure which randomizes traits across all species, but conserves abundance patterns. The conservative nature of our randomization procedure, which keeps abundance patterns in the community static, may contribute to this observed result, and will necessarily be more true for certain test statistics, as illustrated in our seed mass results (Table 1). This will not be the case for similar

observations for test statistics used to examine nominal traits. So the observations that results change in P-value across the α threshold for branching type at both plot sizes, and for fruit type at the 75 × 75 cm plot size, yields stronger support for the assertion that the use of abundance data in analysis can play an important role in testing these patterns.

Interpretations of patterns

While we observed several patterns of deterministic community assembly for the traits examined, a great deal of trait-variation explored did not contribute to significant patterns of over- or underdispersion. Random assembly with respect to these traits may indicate that variation in these traits is unimportant in driving the organization of species within these grassland communities. In particular, it suggests that variation in these traits do not likely contribute to the filtering of species along biomass or moisture gradients in grasslands, or differential resource use in these communities. It is possible that these patterns will differ in other communities, or at different plot sizes than those considered here.

The observed pattern of random species organization with respect to maximum species height (Table 1) is consistent with findings by Schamp et al. (2008) in an old field community, and those of Stubbs & Wilson (2004) for three plot sizes in sand dune communities. However, these results differ from findings by Schamp & Aarssen (2009) for forest communities where tall plant species were overrepresented relative to what was expected by chance, and from findings that coexisting species in wetlands are overdispersed with respect to maximum height (Weiher et al. 1998), and those of Stubbs & Wilson (2004) who observed significant underdispersion with respect to plant height at one plot size. These findings also do not support the theoretical prediction of overdispersion for this trait by Weiher & Keddy (1995). Lastly, effect sizes of our tests for this trait did not vary predictably with plot biomass, while Schamp & Aarssen (2009) observed that taller plant species were overrepresented to a greater degree in more productive forest plots. A multi-community study will be required to determine whether inconsistency in community assembly rules related this trait results from variation along successional gradients, different scales of analysis, or the varied context with which this trait may contribute both to niche differentiation (i.e. overdispersion), or asymmetrical competition, which would lead to underdispersion (Grime 2006, Scheffer & van Nes 2006, Schamp et al. 2008). Coexisting species were also randomly assembled with respect to minimum species height. This trait was examined as a result of its potential advantage in low resource habitats where survival might be improved when resource requirements, which will be size related, are small. It is possible that this trait will be more important in more nutrient limited communities than those studied here.

Coexisting species were also significantly underdispersed at both plot sizes with respect to seed mass; with small species also being significantly overrepresented in our vegetation plots (Table 1); this effect was also prominent within wet grasslands when these were considered separately (Electronic Appendix 5), but not in dry grasslands (Electronic Appendix 4). Evidence suggests that large seeds have a higher probability of successful recruitment than small seeds (Turnbull et al. 1999). Multiple studies, for example, have demonstrated that large seeds have a survival advantage that is more pronounced in shaded habitats (Moles & Westoby 2004, Bruun & ten Brink 2008). Donath & Eckstein (2010), by analogy, found that large-seeded species had a fitness advantage only when seeds were shed beneath a ground cover. Drought is another factor that may be advantageous for large-seeded species (Bruun & ten Brink 2008). As our study system is composed of wet to semi-dry, open mown grasslands, these potential advantages of large seeds may have disappeared, leaving small seeded species with an advantage. This pattern could result from smaller-seeded species having better dispersal ability within grasslands; such an advantage could also be mediated by seed quantity, given that seed mass is generally negatively correlated with seed production (Paul-Victor & Turnbull 2009). A larger number of seeds

could result in a larger number of seedlings, which may be advantageous in mown grasslands where seedling mortality may be high after mowing. Such different responses of functional traits to different vegetation management regimes have been repeatedly demonstrated (e.g. Kahmen & Poschlod 2008, Klimešová et al. 2008); however, management effects are difficult to generalize as some traits may respond non-linearly to different management intensities (Saatkamp et al. 2010). When wet and semi-dry grasslands were considered separately, small seed size appeared to be clearly advantageous within wet grasslands (Electronic Appendix 5). This may illustrate the important contribution of dispersal ability in seed mass convergence, as small wet patches are in fact isolated habitat islands in the matrix of semi-dry grasslands. The important role of dispersal limitation of wetland vascular plants in the discrete spring fen habitat in the study area has been clearly demonstrated in a previous study (Hájek et al. 2011). Nevertheless, small seeds are somehow favoured in semi-dry grasslands as well (Table 3). We also analyzed a larger data set sampled in a single large semi-dry grassland (the Čertoryje Nature Reserve) and found a similar pattern of underdispersion with respect to seed-mass (B. Schamp, E. Hettenbergerová & M. Hájek, unpublished data).

We also observed non-random patterns of dispersion for CGOs; evenness of CGO representation among coexisting species was significantly lower than expected by chance, indicating that some CGO categories were favoured/overrepresented within plots. This finding supports the importance of CGOs as a functional trait that contributes to patterns of community assembly with particular clonal growth organs possibly contributing to a competitive advantage under different abiotic conditions (Wildová et al. 2007, Klimeš 2008, Klimešová & Klimeš 2008). For example, CGO evenness decreased with increasing moisture, indicating that the observed over-representation of some CGOs was accentuated in wet grasslands. While the slope of this relationship is extremely small, this is possibly due to the fact that some CGOs are overrepresented in general, affording limited opportunity for this to be accentuated at one end of a moisture gradient. However, this underdispersion is also observed for CGOs for wet grassland plots, suggesting that even for portions of this gradient, some CGOs are favoured (Electronic Appendix 7). Sosnová et al. (2010) have observed the prevalence of rhizomatous plants in fens and bogs, while other clonal organs are only marginally represented, an observation that may explain these results. Species were randomly organized in plots with respect to lateral spread, another important clonal trait; however, coexisting species were richer in categories for this trait in low-biomass plots (i.e. higher richness; Table 4). This result may suggest a competitive advantage for fast spreading clonal plants in more nutrient-rich habitats (van Groenendael et al. 1996, Sosnová et al. 2010). The plot-level richness of leaf distribution in CGO (rosette, semi-rosette, no rosette) decreased with increasing plot biomass and decreasing soil moisture, which may coincide with the light regime experienced by these plants. Rosette plants are supported in low-productive vegetation with good light penetration through canopy of taller plants and may better survive mowing (Klimeš & Klimešová 2001). Tall grasses such as *Molinia arundinacea* were common dominants in our grasslands, restricting superior rosette plants if their above-ground biomass is high (Lepš 1999, Hájková et al. 2009).

We further demonstrated non-random dispersion of non-clonal nominal traits. Coexisting species had fewer representative pollen vectors and fruit types in fen grasslands (Table 4), characterized by wetter conditions and lower productivity. These conditions coincide with the prevalence of members of the *Cyperaceae*, which are mostly anemogamous plants producing achenes. On the other hand, coexisting species in wet grasslands were slightly richer in flowering phenology; although this pattern was not significant (Table 2), the effect size of this test increased significantly with plot moisture (Table 3). Additionally, flowering phenology was nearly significantly overdispersed when analyses examined only wet grassland plots (Electronic Appendix 7). Obviously, many phenological aspects alternate

in small spring fen grasslands in the study area, starting with *Tussilago farfara* in early spring followed by *Eriophorum angustifolium* and *Dactylorhiza majalis* in spring, *Eriophorum latifolium* and *Epipactis palustris* in summer and *Parnassia palustris* and *Gentianopsis ciliata* in autumn. Evolution of different flowering phenologies may be driven by interactions with pollinators (e.g. Pleasants 1980, Devaux & Lande 2010), but in our case many examined plants are anemogamous and, the effects were lower for neighbouring drier plots. Coexisting plant species may also differ in phenology because flowering generally coincides with peak resource needs, such that species differing in flowering time may also avoid competition, as expected under Limiting Similarity Theory. Our results suggest that this pattern is confined to high moisture, low biomass parts of these grasslands, suggesting that temporal niche partitioning may be more likely under particular environmental conditions. These wet fen grasslands are extremely phosphorus-limited (Rozbrojová & Hájek 2008) and species growing early in spring may gain the advantage in phosphorus uptake, thus the observed pattern for flowering phenology may be driven by a more general growth phenology pattern. Importantly, coexisting plant species were no more or less rich with respect to flowering phenology than would be expected by chance. It is possible that a different observation would be observed for plots at the more extreme end of a low biomass and high moisture gradient. Further studies focused more tightly on particular grassland types are therefore needed.

Additionally, coexisting species possessed a greater variety of fruit types than expected by chance. Fruit type is often strongly phylogenetically conserved and may here be an indicator of phylogenetic overdispersion within plots (e.g. Tofts & Silvertown 2000, Prinzing et al. 2008). On the other hand, this pattern may be related to variable seed dispersal or anti-granivory strategies. While the intent of this study was to examine a large number of traits that may have yet unexplored consequences on community dynamics, where patterns have been observed, further analysis will be necessary to clarify underlying mechanisms for our observed patterns.

See <http://www.preslia.cz> for Electronic Appendix 1–7.

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Souhrn

Studovali jsme uspořádání společenstev ve vztahu k funkčním vlastnostem 216 druhů rostlin. Různě druhově bohatá travinobylinná společenstva jsme snímkovali podél vlhkostního gradientu od subxerothermních luk po vápnitá prameniště slatiniště. Použili jsme tři kontinuální vlastnosti druhů (maximální a minimální výška rostliny, hmotnost semen) a sedm kategoriálních vlastností (květní fenologie, typ plodu, přenos pylu, typ klonálních růstových orgánů, typ větvení, rozložení listů a boční šíření). Některé druhy byly přiřazeny k více než jedné kategorii v dané vlastnosti (např. typ klonálních růstových orgánů). Na dvou různých velikostech ploch (25 × 25 cm a 75 × 75 cm) jsme pomocí nulového modelu testovali, zda je uspořádání společenstev náhodné vzhledem ke studovaným vlastnostem rostlin, a to zvláště pro prezenčně-absenční a zvláště pro kvantitativní data. Na ploše 25 × 25 cm jsme testovali i vliv hmotnosti nadzemní biomasy a vlhkosti půdy na toto uspořádání. Zjistili jsme, že druhy byly ve zkoumaných společenstvech výškově náhodně rozmístěny a převažovaly druhy s lehčími semeny. Tento

výsledek platil pro obě velikosti ploch, při použití jak prezenčně-absenčních, tak i kvantitativních dat. Studovaná společenstva byla nenáhodně uspořádána vzhledem k pěti studovaným vlastnostem (hmotnost semen, typ plodu, typ klonálních růstových orgánů, typ větvení a rozložení listů), avšak pouze výsledek pro typ větvení je v souladu s predikcemi Teorie limitující podobnosti (tj. rozdílnost vlastností v lokálním společenstvu). U typu plodu a typu větvení se výsledky výrazně lišily v závislosti na tom, zda byla použita prezenčně-absenční nebo kvantitativní data. Obecně ale platí, že výsledky byly stejné pro obě velikosti plochy, což naznačuje, že malá změna ve velikosti plochy nemá na výsledky analýz vliv. Pro některé testované vlastnosti jsme potvrdili významný vztah mezi rozložením vlastností rostlin ve společenstvu a produkcí biomasy nebo vlhkostí půdy, což naznačuje, že zákonitosti uspořádání společenstva vzhledem k různým funkčním vlastnostem rostlin mohou být závislé na množství produkované biomasy a na vlhkosti půdy. Když jsme datový soubor rozdělili podle vlhkosti, popisované nenáhodné rozmístění vlastností rostlin se mnohem více projevilo ve společenstvech slatinišť než subxerothermních luk, a to nejvíce v případě velikosti semen.

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Supplementary Materials

Electronic Appendix 1. Explanation of used traits. Source: 1) Kubát et al. (2002), 2) Fitter & Peat (1994), Royal Botanic Gardens Kew (2008), Moles et al. (2005), Institute of Botany of the ASCR (2010), 3) Klotz et al. (2002), 4) Klimešová & Klimeš (2006, 2008), Klimešová & de Bello (2009).

Plant traits	Source	Explanation
Maximum height	1	maximum species height
Minimum height	1	minimum species height
Seed mass	2	weight of seeds
Flowering phenology	3	values 0-10 according to vegetation period
Fruit type	3	berry lomentum legume capsule nut aggregate follicles aggregate nutlets siliqua schizocarp vegetative
Pollen vectors	3	pollination by wind selfing by a neighbouring flower pollination by insects pollination by slugs spontaneous pollination within a flower selfing in unopened, rudimentary flower selfing in unopened flower
Clonal growth organs	4	stem tuber turion plantlet (pseudovivipary) plant fragment of stem origin epigeogenous stem (rhizome) hypogeogenous stem (rhizome) stem tuber bulb root-splitter roots with adventitious buds root tuber offspring tuber at distal end of above-ground stem
Branching type	4	monopodial sympodial dichotomous
Leaf distribution	4	no rosette semi-rosette rosette
Lateral spread (m/yr)	4	< 0.01 0.01–0.25 > 0.25 dispersable

Electronic Appendix 2. A summary of the mean percentage of species in each plot for which data on each trait was missing. For presence-absence data, this was calculated as the number of species missing trait data for a given plot divided by the total number of species in that plot (i.e. plot richness); the mean of this plot-level value across plots is presented below. For abundance data, the same measure was calculated, but weighted by abundance.

Plot size (cm)	Average data missing per plot			
	Presence-absence		Abundance	
	25×25	75×75	25×25	75×75
Maximum height	0.9%	0.7%	0.9%	0.7%
Minimum height	0.9%	0.7%	0.9%	0.7%
Seed mass	2.9%	2.9%	2.2%	2.3%
Flowering phenology	4.5%	4.6%	5.5%	5.3%
Fruit type	0.9%	0.8%	0.9%	0.8%
Pollen vectors	0.9%	0.9%	1.0%	0.9%
Clonal growth organs	1.6%	1.6%	1.6%	1.5%
Branching type	4.1%	4.3%	1.5%	2.0%
Leaf distribution	1.0%	0.8%	1.0%	0.9%
Lateral spread	1.9%	2.4%	1.7%	2.1%

Electronic Appendix 3. Results from a sensitivity analysis investigating the impact of missing trait data on results. This test was conducted using flowering phenology, the trait with the highest proportion of missing trait data. This analysis used only plots that contained species for which flowering phenology is known (25 × 25 cm: 68 plots; 75 × 75 cm: 38 plots).

Plot size	No. plots	Test statistic	Presence-absence		Abundance	
			Obs > Exp	Obs < Exp	Obs > Exp	Obs < Exp
25×25 cm	68	Richness	0.880		0.908	
		Evenness	0.121		0.179	
75×75 cm	38	Richness	0.512		0.517	
		Evenness	0.774		0.632	

Electronic Appendix 4. Results from trait dispersion analysis on three continuous species-level traits: maximum height, minimum height (minimum size at reproduction), and seed mass. These analyses focused only on 51 dry grassland plots; analyses used presence-absence and abundance data from 126 plots for each of two plot sizes (25 × 25cm, 75 × 75cm). P-values indicate whether plots are overdispersed (Obs > Exp), or underdispersed (Obs < Exp) for the trait of interest. Bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

Plot size (cm)	Test statistic	Presence-absence				Abundance			
		Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp	
		25×25	75×75	25×25	75×75	25×25	75×75	25×25	75×75
Maximum height	Mean	0.882	0.750			0.736	0.569		
	Range			0.657	0.840			0.678	0.866
	Mean NTD	0.865	0.660			0.886			0.838
	Var NTD			0.608	0.687			0.678	0.982
Minimum height	Mean	0.343	0.560			0.154	0.179		
	Range	0.242	0.356			0.225	0.352		
	Mean NTD	0.201	0.342			0.720	0.907		
	Var NTD	0.834	0.980			0.245	0.840		
Seed mass	Mean			0.606 ψ	0.414 ψ			0.648 ψ	0.602 ψ
	Range	0.668 ψ			0.466 ψ			0.694 ψ	0.493 ψ
	Mean NTD	0.737 ψ			0.742 ψ	0.278	0.660		
	Var NTD			0.279 ψ	0.698 ψ	0.592	0.595		

ψ change in significance from full analysis

Electronic Appendix 5. Results from trait dispersion analysis on three continuous species-level traits: maximum height, minimum height (minimum size at reproduction), and seed mass. These analyses focused only on 52 wet grassland plots; analyses used presence-absence and abundance data from 126 plots for each of two plot sizes (25 × 25cm, 75 × 75cm). P-values indicate whether plots are overdispersed (Obs > Exp), or underdispersed (Obs < Exp) for the trait of interest. Bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

Test statistic	Presence-absence				Abundance				
	Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp		
	25×25	75×75	25×25	75×75	25×25	75×75	25×25	75×75	
Maximum height	Mean			0.271	0.357			0.276	0.368
	Range			0.776	0.692			0.794	0.668
	Mean NTD	0.611	0.712					0.465	0.850
	Var NTD	0.562	0.544					0.815	0.926
Minimum height	Mean			0.090	0.130			0.154	0.189
	Range	0.890			0.959	0.866			0.942
	Mean NTD	0.491	0.773			0.910	0.714		
	Var NTD	0.507	0.487					0.756	0.578
Seed mass	Mean			0.032	0.005			0.084 ψ	0.034 ψ
	Range			0.023	0.002			0.022 ψ	0.007 ψ
	Mean NTD			0.013	0.006	0.707	0.398		
	Var NTD			0.045	0.114 ψ			0.542	0.913

Electronic Appendix 6. Results from trait dispersion analysis on seven nominal traits for only dry grassland plots (51 plots). P-values indicate whether plots are richer (Richness: Obs > Exp), or poorer (Richness: Obs < Exp) in terms of variation in these traits, and whether these traits are more evenly (Evenness: Obs > Exp), or less evenly (Evenness: Obs < Exp) distributed within plots. Studied traits include flowering phenology (month of flowering), fruit type, pollen vector, leaf distribution, clonal growth organ and branching type. The last four of these traits are unique in that a single species can have multiple values; for example, a species may be both insect and wind pollinated. This was incorporated into the analysis. Bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

Test Statistic	Presence-absence				Abundance				
	Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp		
	25×25	75×75	25×25	75×75	25×25	75×75	25×25	75×75	
Flowering phenology	Richness			0.102	0.552			0.094	0.567
	Evenness	0.265			0.836	0.114			0.619
Fruit type	Richness			0.470	0.729			0.480	0.714
	Evenness			0.064 ψ	0.507			0.005	0.217 ψ
Pollen vectors	Richness	0.682			0.753	0.742			0.761
	Evenness	0.789			0.770	0.642			0.628
Clonal growth organ	Richness			0.627	0.728			0.646	0.722
	Evenness			0.487 ψ	0.491 ψ			0.145 ψ	0.206 ψ
Branching type	Richness	0.296			0.168 ψ	0.260	0.257		
	Evenness		0.847 ψ	0.112 ψ		0.046ψ			0.038ψ
Leaf distribution	Richness			0.016	0.001			0.016ψ	0.001
	Evenness	0.002	0.001			0.002	0.001		
Lateral spread	Richness			0.442	0.096			0.437	0.101
	Evenness			0.171	0.130			0.118	0.148

ψ change in significance from full analysis

Electronic Appendix 7. Results from trait dispersion analysis on seven nominal traits for wet grassland plots (52 plots). P-values indicate whether plots are richer (Richness: Obs > Exp), or poorer (Richness: Obs < Exp) in terms of variation in these traits, and whether these traits are more evenly (Evenness: Obs > Exp), or less evenly (Evenness: Obs < Exp) distributed within plots. Studied traits include flowering phenology (month of flowering), fruit type, pollen vector, leaf distribution, clonal growth organ and branching type. The last four of these traits are unique in that a single species can have multiple values; for example, a species may be both insect and wind pollinated. This was incorporated into the analysis. Bold values signify type-I error rates at $\alpha < 0.05$ (i.e. P-values).

	Test Statistic	Presence-absence				Abundance			
		Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp	
Plot size (cm)		25×25	75×75	25×25	75×75	25×25	75×75	25×25	75×75
Flowering phenology	Richness	0.415	0.577			0.410	0.581		
	Evenness	0.055	0.092			0.111	0.130		
Fruit type	Richness			0.333	0.220			0.354	0.148
	Evenness			0.060	0.197			0.037	0.196 ψ
Pollen vectors	Richness		0.940	0.436 ψ		0.927	0.439		
	Evenness	0.990			0.897			0.711 ψ	0.464
Clonal growth organ	Richness		0.735	0.624		0.723	0.640		
	Evenness			0.020	0.023			0.007	0.005
Branching type	Richness	0.180	0.173 ψ			0.201	0.171		
	Evenness			0.256 ψ	0.287 ψ			0.312	0.363
Leaf distribution	Richness			0.230 ψ	0.188 ψ			0.217	0.182 ψ
	Evenness	0.025	0.045			0.013	0.060 ψ		
Lateral spread	Richness			0.933	Iv*			0.955	Iv*
	Evenness			0.776	0.770			0.657	0.601

*Insufficient variation to test; ψ change in significance from full analysis

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Prezentace výsledků na tuzemských a zahraničních setkáních doktorských studentů (v letech 2006, 2007, 2010 a 2011).