

Phylogenetic structure of plant species pools reflects habitat age on the geological time scale

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Keywords

Central Europe; Environmental filtering; Evolution; Phylogenetic diversity; Plant community; Species pool; Vegetation type

Abbreviations MPD = mean phylogenetic distance; PS = phylogenetic structure.

Nomenclature

Durka & Michalski (2012)

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Introduction

Patterns of phylogenetic relatedness of species within and across communities, known as phylogenetic structure (PS), have recently become an important research focus because of their potential to improve our understanding of community assembly (Webb et al. 2002; Cavender-Bares et al. 2009). Namely, the information on shared ancestry (phylogenetic relationship of taxa) is sometimes used as a proxy for the extent to that species share common traits, which can be useful for identification of trait-based ecological processes, abiotic filters or species interactions when traits are difficult to identify (Leibold et al. 2010; Mayfield & Levine 2010; Peres-Neto et al. 2012; Butterfield et al.

Abstract

Question: Patterns of phylogenetic relatedness of species within community types (phylogenetic structure; PS) are often used to infer processes of community assembly, yet the causes of these patterns remain poorly understood. Here we ask whether PS of extant plant species pools is related to availability of correspoding habitats in the geological history.

Location: Czech Republic.

Methods: We characterized PS of recent species pools of 88 major vascular plant community types occurring in the country, comprising a total of 2306 species, using the mean phylogenetic distance (MPD) between all pairs of species found in each species pool, and compared the PS of these species pools with the relative ages of their habitats.

Results: Clustered PS was observed consistently in species pools of historically younger community types of grasslands and other open habitats, which were formed mainly during the late Tertiary as a consequence of climate aridization and cooling, and to which only a limited number of lineages had enough time to adapt. Clustered PS was also typical of species pools of the recent human-made habitats, in which it probably resulted from environmental filtering of pre-adapted lineages. In contrast, overdispersed PS was observed in forests and other plant community types occurring in habitats that are assumed to have existed continuously since the Mesozoic.

Conclusions: Our analyses suggest that habitat age has a strong effect on PS of species pools of extant plant community types. Based on these results, we argue that history of the analysed species pools at a geological time scale should be considered whenever differences in PS are discussed and interpreted.

2013; Gerhold et al. 2015). There are two types of deterministic processes which drive species composition of plant communities: (i) abiotic processes, usually understood as environmental filters, which select those species of the regional flora that match the specific habitat requirements (Silvertown et al. 2006); and (ii) biotic processes, which operate on finer scales and lead to competitive exclusion of species that are too similar in resource use and growth patterns (Silvertown et al. 2006; Emerson & Gillespie 2008). Both types of processes may generate the same general patterns of phylogenetic structure of plant communities. For example, clustered PS is usually assumed to result from environmental filtering of phylogenetically related species sharing the same traits (Webb et al. 2002), but it may also result, somehow paradoxically, from interspecific competition (Mayfield & Levine 2010). In contrast, overdispersed PS is usually believed to result from competitive exclusion between closely related species with similar resource use strategy (Webb 2000; Webb et al. 2002; Kembel & Hubbell 2006). However, the studies that assessed effect of competition on exclusion of related species did not detect any relationship between competition and phylogenetic overdispersion (Brunbjerg et al. 2012; Bennet et al. 2013; see also Gerhold et al. 2015). Other possible explanations of overdispersed PS are facilitation between distantly related species (Valiente-Banuet & Verdú 2007) or environmental filtering of convergent life strategies evolved in divergent phylogenetic lineages (Webb et al. 2002; Prinzing et al. 2008).

Current knowledge of the processes that affect phylogenetic structure of plant communities remains limited either to the fine scale of vegetation plots (e.g. Letcher 2010; Brunbjerg et al. 2012; Letcher et al. 2012) or to regional floras (Bartish et al. 2010; Yan et al. 2013). Recent studies on these scales suggested that habitat age is an important factor affecting PS (Gerhold et al. 2015). There are some indications that phylogenetic diversity of plant species pools tends to increase with the age of their respective habitats (see Zobel et al. 2011 for an example from the Canary Islands), but reliable studies comparing species pools of multiple community types on the regional scale are still missing.

Here we aim to contribute to the understanding of PS patterns by analysing species pools of vascular plant community types on a regional scale. Species pool is a set of species that are potentially capable of co-existing in a particular community (Zobel 1997). Different habitats and plant communities occurring in these habitats have their specific species pools. The species pool concept is convenient for studying effects of environmental filters on plant community assembly because species assignment to a particular species pool reflects the ability of this species to establish in a specific habitat. In contrast to data from vegetation plots in which species co-occur and directly compete, species included in the same species pool do not need to co-occur at the same site, although they occur in the same habitat in a larger region. The species pool-based approach thus makes it possible to focus on effects of abiotic environmental filters on PS (Lessard et al. 2012) while disregarding effects of interspecific interactions.

Making an intuitive prediction that the number of species and of lineages adapted to a given, continuously existing habitat will increase over evolutionary time, we may expect specific relationships between PS and habitat age. Habitats that are relatively young on the geological time scale should host community types with clustered PS because (i) only a few lineages from the existing species pool are preadapted to these habitats, and (ii) the time was too short to allow for successful adaptation of a broader spectrum of distantly related lineages (Fig. 1a). Presumably these habitats would be cold- and drought-stressed because such habitats were absent or rare during the past geological periods characterized by a globally warm and humid climate (Wiens et al. 2010). With many different lineages becoming adapted to the habitat, the PS may be driven mainly by stochastic dispersal processes (Ozinga et al. 2005; Fig. 1b) and, consequently, become random. Co-existence of species in old habitas may lead to the competitive exclusion of closely related species resulting from their similarity in the resource use strategy (Fig. 1c: i). Alternatively, the contraction or disappearance of ancient habitats in a given region may cause decline (Fig. 1c: ii) or extinction (Fig. 1c: iii) of early diverging phylogenetic lineages unless they are able to re-adapt to modern habitat types. These processes may cause deletion of species on different branches of the phylogenetic tree, thus increasing phylogenetic distances between species, resulting in phylogenetic overdispersion. It is obvious that the age of habitats drives recent species composition because species pools of older habitats can be built from a wider range of major lineages, whereas species pools of younger habitats are limited to a few lineages which have undergone diversification (Gerhold et al. 2008, 2015).

To test the hypothesis of the relationship between PS and habitat age we first assess PS across species pools of a wide range of Central European plant community types. To our knowledge, the data set used in our study is the most comprehensive source of information on regional species pools across an entire range of plant community types at a national scale. As a next step, we estimate the age of the respective habitats. By comparing the observed PS of species pools with the estimated ages of their respective habitats we explore the hypothesized relationship between PS and habitat age. Finally, by comparing the pattern of PS between all vascular plants and angiosperms



Fig. 1. Conceptual representation of the factors that might determine phylogenetic structure of extant species pools. Each hypothetical phylogenetic tree contains three subtrees showing different causes of the given phylogenetic structure. Species belonging to the species pool of the same habitat type have the same colour; for red and green species pools (middle and right subtrees, respectively) a possible evolution from clustered to overdispersed phylogenetic structure may be seen with increasing age of their habitats.

only, we aim to gain insight into the factors underlying PS of particular species pools.

Methods

Plant community data

A database of regional species pools for 88 broadly defined habitat types (and corresponding plant community types) of the Czech Republic (78 000 km²) was used as the data

source (Sádlo et al. 2007). This database comprises all the major plant community types of the country, thus representing vegetation diversity of inland temperate Europe in a transitional zone between suboceanic and subcontinental climate except for some alpine plant community types (Ellenberg 1988; Chytrý 2012). Species pools were defined based on the species composition data from 24 283 geographically stratified vegetation plots assigned to different habitat types (for further details see Sádlo et al. 2007). The

database contained 2347 vascular plant species or subspecies, but for the analysis all subspecies were aggregated to the species level, resulting in a total of 2306 species. Species were assigned to four frequency classes: (1) rare; (2) common; (3) dominant; and (4) highly characteristic dominant species (e.g. species which determine the general appearance of the community type, such as *Calluna vulgaris* in heathlands; see Sádlo et al. 2007). As PS strongly depends on whether the very old lineages (e.g. gymnosperms) are included or excluded (Kembel & Hubbell 2006; Letcher 2010), the PS analyses were carried out separately for all vascular plants (including lycopodiophytes, ferns, horsetails, gymnosperms and angiosperms) and for angiosperms only.

Phylogenetic data

A dated, ultrametric phylogeny was prepared for the 2306 studied vascular plant species by pruning the DaPhnE 1.0 supertree of the Northwest and Central European vascular plant species (Durka & Michalski 2012). Taxa that were not included in the supertree (n = 220, mainly species, but also a few genera; e.g. Crypsis, Ligularia) were supplemented manually to the existing nodes of the DaPhnE tree. The supplemented nodes always represented the latest known common ancestor of the added taxon, and the added taxon always created a polytomy at this node. The decision on the common ancestry was based on the taxonomic information published in the Flora of the Czech Republic (Hejný et al. 1988; et seq.) and the Checklist of vascular plants of the Czech Republic (Danihelka et al. 2012). The species concepts and the nomenclature follow those used in the original DaPhnE 1.0 supertree (Durka & Michalski 2012).

Phylogenetic structure of species pools

For each of the 88 species pools, we calculated the mean phylogenetic distance (MPD; Webb et al. 2002) between all species pairs. As the analyses are based on presences/ absences, our MPDs correspond to phylogenetic distinctness (Hardy & Senterre 2007; Hardy et al. 2012).

To assess whether species pools were composed of species more closely (or distantly) related to each other than expected from a random draw of species from the regional flora (n = 2306 species), we compared the observed MPD values with the MPD values from 999 random species pools. Random species pools were generated using the null model '1a' of Hardy (2008) by shuffling the species names across the branch tips of the full tree with 2306 species. Permutations were restricted within groups of species that had similar overall occurrence frequencies across the 88 species pools; whereby the maximum/minimum occurrence frequency ratio within each frequency class was equal to 4 (see Hardy 2008; Purschke et al. 2013). This type of null model maintains (i) the number of species within each species pool, (ii) the frequency of occurrence of the species across all species pools, and (iii) the phylogenetic signal in overall species frequencies across the phylogeny.

The standardized effect size (MPD SES) was calculated according to Gotelli & Rohde (2002):

MPD SES = $(MPD_{obs} - meanMPD_{rand})/sdMPD_{rand}$,

where MPD_{obs} is the observed MPD for a given species pool, meanMPD_{rand} the mean of the MPD values obtained for the random species pool, and sdMPD_{rand} is the SD of the MPD values of the random plant species pools. Higher than expected values of MPD (MPD SES > 1.96) indicate that species within a particular species pool are more distantly related than expected by chance, indicating phylogenetic overdispersion. Lower than expected values (MPD SES < 1.96) indicate that species within a pool are more closely related than expected by chance, indicating phylogenetic clustering. Analysis of PS was carried out in the R statistical package (R Foundation for Statistical Computing, Vienna, AT), using the libraries 'picante' (Kembel et al. 2010) and 'spacodiR' (Eastman et al. 2011). The PS analyses were calculated separately for all vascular plant species and for angiosperms only.

We identified nodes that had a significant effect on PS of species pools. To identify clades with significant affinities to particular species pools, we used the *nodesig* procedure in Phylocom (Webb et al. 2008). This procedure tests whether a particular node in the phylogeny has significantly more or less daughter taxa, i.e. is over- or underrepresented in a species pool compared to the null model prediction (Webb et al. 2008; Letcher 2010).

Theoretically, PS of species pools might reflect the inherent ecological variability among plots representing a particular community type. To account for this, we measured inherent variability in species composition among all plots representing a particular community type by taking the mean of pair-wise Jaccard dissimilarity indices (Whittaker 1975). The Jaccard dissimilarity index between two plots is defined as:

$$J = 1 - a/(a+b+c)$$

where *a* is the number of species shared, *b* is the number of species unique to the first plot, and *c* is the number of species unique to the second plot. *J* ranges between 0 and 1, where 0 indicates identical species composition of the two

plots, and 1 indicates that the two plots have no species in common. The calculations were done using JUICE 7.0 (Tichý 2002). We related MPD to the inherent variability within community types (mean of Jaccard dissimilarity indices) using linear regression. The regression was calculated separately for all vascular plants and for angiosperms only using *lm* function, in R package 'base'.

Estimation of habitat age

Estimating habitat age and its continuity over large time scales that enable speciation and evolution of phylogenetic lineages is a difficult issue. Therefore, we considered it only in relative terms based on the approximate duration of particular habitats as inferred from the fossil record (Table 1). A very young age is assumed for vegetation of open human-made habitats that have not existed longer than a few thousand years (Zohary 1996). Fossil records and phylogenetic evidence also indicate that open grasslands are not older than mid-Tertiary, when they were formed due to opening of the closed Palaeogene forests (Linder & Rudall 2005; Stromberg 2011) as a response to global cooling and drying (Zachos et al. 2001). Forests are assumed to be older than grasslands. They were the dominant vegetation in Europe until the late Cretaceous and lower Tertiary, and only later were replaced with grasslands in many areas (Mai 1995; Stromberg 2011). A long continuity and corresponding high age can also be assumed for some types of azonal habitats such as wetlands and water bodies that may have persisted in a landscape, although at changing sites, for ages (Table 1).

We compared PS of species pools among groups of habitats of different age using the Kruskal-Wallis ANOVA with the Nemenyi post-hoc tests using the R library *PMCMR* (http://cran.r-project.org/web/packages/PMCMR/index.html.

Results

Of the 88 vascular plant species pools analysed, 31 (35%) were phylogenetically clustered, 36 (41%) random and 21 (24%) overdispersed (Table 2). The analysis of angiosperms only yielded similar results: 37 (42%) clustered, 37 (42%) random and 14 (16%) overdispersed (Table 2).

Consistently in both data sets, phylogenetic structure of species pools was related to the estimated habitat age (Fig. 2). Clustered PS was observed in species pools of plant communities occurring in very young, human-made habitats, such as arable fields, ruderal and trampled sites, and also in older but still relatively young habitats such as grasslands (including wet, mesic, dry, sand and saline types), herbaceous fringes of lowland rivers, xeric scrub and thermophilous oak forests (Fig. 2, Appendix S1). In contrast, random or overdispersed PS was consistently found in species pools of ancient habitats. For the data set of all vascular plants, overdispersed PS was detected for most forest, spring and mire species pools. The additional analyses showed that this was due to the frequent presence of relatively old phylogenetic lineages such as lycopodiophytes, ferns and gymnosperms. In the analyses of angiosperms only the overdispersed PS disappeared for most of these species pools. Analogously to the data set of all vascular plants, the overdispersed PS detected for angiosperm species pools of some aquatic, wetland, riverine and springs habitats, willow carrs and some forests (Appendix S1) was mainly caused by the presence of taxa from ancient angiosperm lineages (e.g. Alismatales, Nymphaeaceae and Myriophyllaceae for aquatic habitats). Taxa contributing significantly to the phylogenetic structure of the studied species pools are listed in Appendix S2.

We found no relationship between inherent variability of community types and phylogenetic structure of their

Table 1.	Age estimations	of habitats of particular	aggregated plant co	ommunity types and	I major events that influe	nced the habitat development.
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Aggregated Community Type	Habitat Age of Aggregated Community Type	Major Events	References
Cliffs, Screes and Walls	Uncertain (Cliffs, Screes); Neolithic or younger (Walls)		
Alpine and Sub-alpine Vegetation	Mid-Tertiary	Global cooling and drying; Alpine orogeny	Mai (1995)
Aquatic Vegetation	Cretaceous or older		Coiffard et al. (2012)
Wetland and Riverine Vegetation	Cretaceous or older		Coiffard et al. (2012)
Spring and Mire Vegetation	Late-Tertiary	Northern hemisphere climate cooling	Shaw et al. (2010)
Mesic and Wet, Nutrient-rich Grasslands	Late-Tertiary	Global cooling and drying	Stromberg (2011)
Mesic, Nutrient-poor Grasslands	Late-Tertiary	Global cooling and drying	Stromberg (2011)
Dry Grasslands and Steppes	Late-Tertiary	Global cooling and drying	Stromberg (2011)
Sand Grasslands	Late-Tertiary	Global cooling and drying	Stromberg (2011)
Vegetation of Saline Soils	Tertiary	Existence of salt-rich sediments	Ellenberg (1988)
Heathlands and Scrub	Uncertain		
Forests	Cretaceous or older		Mai (1995), Wang et al. (2009)
Ruderal and Weed Vegetation	Neolithic or younger	Frequent and regular disturbance	Zohary (1996)

Aggregated Community Type	Vascular Plants (%)			Angiosperms (%)		
	Clustered	Random	Overdispersed	Clustered	Random	Overdispersed
Cliffs, Screes and Walls	0	1 (25)	3 (75)	4 (100)	0	0
Alpine and Sub-alpine Vegetation	0	2 (100)	0	2 (100)	0	0
Aquatic Vegetation	0	3 (100)	0	0	1 (33)	2 (67)
Wetland and Riverine Vegetation	2 (17)	10 (83)	0	2 (17)	4 (33)	6 (50)
Spring and Mire Vegetation	0	5 (63)	3 (37)	0	7 (88)	1 (12)
Mesic and Wet, Nutrient-rich Grasslands	6 (86)	1 (14)	0	3 (43)	4 (57)	0
Mesic, Nutrient-poor Grasslands	1 (50)	1 (50)	0	2 (100)	0	0
Dry Grasslands and Steppes	4 (67)	2 (33)	0	6 (100)	0	0
Sand Grasslands	5 (100)	0	0	5 (100)	0	0
Vegetation of Saline Soils	1 (25)	3 (75)	0	0	4 (100)	0
Heathlands and Scrub	3 (38)	3 (38)	2 (24)	5 (63)	2 (24)	1 (13)
Forests	4 (20)	4 (20)	13 (60)	1 (5)	15 (75)	4 (20)
Ruderal and Weed Vegetation	5 (83)	1 (17)	0	6 (100)	0	0

 Table 2.
 Numbers and percentages of species pools of individual plant community types with clustered, random or overdispersed phylogenetic structure, summarized over the aggregated community types. See Appendix S1 for details on individual species pools.



Fig. 2. Standardized effect size of mean phylogenetic distance (MPD SES) for species pools, divided into three categories according to the habitat age. Habitats with uncertain age are not included. The same letters indicate homogeneous groups according to the Kruskal-Wallis ANOVA followed by Nemenyi post-hoc tests at P < 0.05. The central line of each box refers to the median, box height to the interquartile range, whiskers to the non-outlier range (1.5 times the interquartile range at each side), and small circles to outliers.

species pools ($R^2 = 0.0408$, P = 0.059 for all vascular plants; $R^2 = 0.0002$, P = 0.89 for angiosperms only). This indicates that PS of ecologically more heterogeneous species pools defined for broader ranges of environmental conditions was not different from PS of more homogeneous species pools related to environmentally homogeneous habitats.

Discussion

Our analysis suggests that a substantial part of the variation in phylogenetic structure across species pools of different plant community types is associated with the age of the respective habitats (Fig. 2). Therefore, habitat age at a geological time scale should be considered whenever differences in PS among plant communities are discussed and interpreted.

Phylogenetically clustered species pools are typical of young habitats

The clustered PS is typical of species pools of relatively young habitats. This clustering likely reflects that during limited evolutionary time, only a few lineages, now represented by large proportions of species in these pools, were able to effectively adapt to these habitats. Although several previous studies reported the correspondence of young habitat age and clustered community structure, these findings were based on small sets of species and limited spatial or temporal scales, mainly on comparisons of early and late stages of ecological succession. For example, overdispersed vs clustered PS was documented in older vs younger successional stages of tropical forests, respectively (Letcher 2010; Letcher et al. 2012; but see Zobel et al. 2011). Shifts from clustered to overdispersed PS were reported for

vegetation succession on dunes (Brunbjerg et al. 2012), as well as for transitions from arable land to grassland (Purschke et al. 2013). On broader spatial scales, alpine grassland plant communities of cold and dry areas of the Qinghai-Tibetan Plateau were shown to be phylogenetically clustered, whereas moist and warm areas in this region were covered with phylogenetically overdispersed forest communities (Yan et al. 2013). The above examples, together with our results, indicate that clustered phylogenetic structure is related to young habitat age. However, we suggest that the main cause is not successional age of the habitat. Instead it is the habitat's age on the geological time scale that provided either more or less time for evolution and diversification of adapted lineages that currently comprise the species pool (and 'lineage pool') of the modern habitat types. Patterns observed in successional series result from the fact that early successional stages usually correspond to evolutionarily young habitats and late stages to ancient habitats.

Ruderal and weed community types occupy the youngest habitats of Central Europe. Their existence depends on human activities and they experienced dramatic expansion, especially after the introduction of Neolithic agriculture, which started in Central Europe about 7000-8000 yrs before present (Zohary 1996). Their species pools are especially rich in species from certain lineages, e.g. Amaranthaceae, Brassicaceae, Fabaceae, Asteraceae or Polygonaceae (for details see Appendix S2). Some recent phylogenetic studies (e.g. Schuster et al. 2013) suggest that the high species richness of these groups is not a result of massive Quaternary radiation in these young habitats. The species pools of these habitats must have been assembled through environmental filtering from already existing pools of preadapted species. Original habitats of these species may have been locally disturbed places in the open Pleistocene landscapes, such as sediment accumulations along rivers, watering places and other sites of large herbivore gatherings, or campsites of Palaeolithic hunter-gatherers.

Clustered PS was also found in species pools of most types of Czech treeless habitats, including wet, mesic, dry, sand and saline grasslands. Such results accord with findings of Bartish et al. (2010) and are in full agreement with theoretical predictions of phylogenetic clustering of coldand drought-tolerant species (mostly confined to grasslands) of Wiens et al. (2010). This is because most clades of current species originated during the time when tropical environments predominated on the planet. Because ecological traits (e.g. cold tolerance) are often phylogenetically conserved, few clades have crossed ecophysiological barriers to colder environments during the subsequent global cooling, resulting in phylogenetic clustering in young habitats. The divergence of the modern cool climate grasses (subfamily *Pooideae*) dates back to the Oligocene (Bouch-

enak-Khelladi et al. 2010) and relates perhaps to the Oligocene climate minimum. Since that time, cool climate grasses experienced a dramatic diversification and range expansion (currently over 3000 species are recognized worldwide; Linder & Rudall 2005), now being dominant in almost all types of open temperate vegetation. Similar radiation to the newly arising open and drought-stressed habitats following the Oligocene climatic minimum occurred in some other groups of advanced angiosperms (e.g. Asteraceae, Brassicaceae, Fabaceae, Cyperaceae; Ford et al. 2006; Franzke et al. 2011), which are now frequent components of modern temperate grasslands. In contrast to the humanmade habitats that appeared perhaps too quickly for plant lineages to evolve appropriate adaptations, the clustered structure of grasslands seems to result from an assembly of lineages that have been continuously adapting to this habitat since the Oligocene (i.e. during the last \approx 30 Myr).

Besides species pools of human-made habitats and grasslands, clustered PS was also found for species pools of thermophilous oak forests (in contrast to the other forest types, which had random or overdispersed PS) and xeric scrub. It seems that the clustered PS of these dry and rather open woody plant community types results from the fact that a considerable part of their species pools is shared with species pools of spatially adjacent dry grasslands (Sádlo et al. 2007).

Phylogenetically overdispersed species pools of all vascular plants: co-existence of plant strategies over an evolutionary time scale

Overdispersed PS within the data set of all vascular plants was associated with presence of species from very old lineages, such as lycopodiophytes, ferns or gymnosperms. The distinctiveness of these ancient taxa and the corresponding large phylogenetic distances to the majority of other taxa, represented by modern angiosperms, always resulted in a substantial increase in MPD and often also in the significantly overdispersed PS of the species pool if more ancient taxa were present. One group of such species pools was that of forests containing gymnosperm trees and several species of ferns; another group was species pools of cliffs, walls, sub-alpine habitats and mires, all relatively rich in ferns. The dramatic effect of presence of ancient taxa on the overall PS can be best documented by removing them from the analysis. After their removal, the overdispersed PS changes to random in species pools of most forest and mire types, or even to clustered in the case of some non-forest habitat types of supposedly young age, such as walls or sub-alpine vegetation (walls appeared with humans and sub-alpine vegetation was formed in Eurasia as a consequence of orogenic processes in the mid-Tertiary). These results clearly point to the sensitivity of the phylogenetic analyses such as those based on MPD to the inclusion of old phylogenetic lineages. They also indicate that overdispersion is not a necessary outcome of competition between close relatives, as suggested also by Bennet et al. (2013). The association between the presence of ancient lineages in a species pool and the overdispersed PS may result from two evolutionary historical processes. First, these species pools occur in refugial habitat types to which ancient lineages are well adapted and where they are still not outcompeted by omnipresent angiosperms. Second, some ancient lineages successfully readapted to modern kinds of habitat, such as leptosporangiate ferns that adaptively radiated into new niches in the angiosperm-dominated forests (Schneider et al. 2004) or poikilohydric ferns (e.g. Asplenium, Polypodium, Notholaena) whose extreme dessication tolerance enables them to persist in drought-stressed and low-productive habitats such as cliffs and walls.

Phylogenetically overdispersed species pools of angiosperms: refuges of early diverging lineages

In the angiosperm data set the contributions of individual species to the overdispersed PS were much more homogeneous than in the data set of all vascular plants. Still, the species pools with overdispersed PS (those of aquatic and wetland habitats, alder carrs, alluvial and beech forests) were generally those rich in species of early diverging (old) angiosperm lineages. This was mainly the case of the aquatic environment harbouring early diverging lineages of angiosperms (Nymphaeaceae) and early diverging lineages of monocots and dicots (Acoraceae, Alismataceae, Araceae, Butomaceae, Ceratophyllaceae, Potamogetonaceae and Ranunculaceae). In the late Cretaceous, aquatic environments and wetlands were the first habitats to become dominated by angiosperms (Coiffard et al. 2012). These environments perhaps persisted continuously and remained generally unchanged until the present, hence they may have served as a refuge of ancient angiosperm groups, which show limited capacity to adapt to other types of modern terrestrial, droughtstressed habitats.

The origin of angiosperm-dominated forests dates back to the late Cretaceous and coincides with the radiation of the rosid clade (108–83 Myr ago; Wang et al. 2009), which includes the majority of modern lineages of angiosperm woody plants (e.g. *Betulaceae*, *Fabaceae*, *Fagaceae*, *Rosaceae* and *Ulmaceae*). Angiosperm-dominated forests became the worldwide dominant vegetation in the favourable climate of the early Tertiary, with tropical or subtropical evergreen forests dominating the vegetation of Central Europe till the mid-Miocene (Mai 1995). The long-term existence of these forests provided enough time for successful adaptation of most of the modern angiosperm lineages. This can be assumed as the major reason for the random PS observed in species pools of most forest types, with the exceptions of alder carrs, alluvial forests and species-rich beech forests, all with overdispersed PS. In the case of carrs and alluvial forests this overdispersion is mostly due to the presence of ancient lineages of wetland monocots (Acoraceae, Araceae and Alismataceae). In the case of species-rich beech forests and alluvial forests this is mainly due to relatively high species richness of lilioid plants (Liliaceae and Orchidaceae), representing an early diverging lineage of monocots, and of angiosperms as a whole. Hence the overdispersed PS of forests seems to result mainly from niche conservatism in the ancient angiosperm lineages and their persistent affinity to ancient types of shady, wet habitats. This type of PS reflects mainly a long-term and continuous persistence of habitat conditions that allow survival of ancient lineages of angiosperms, which otherwise have a limited ability to adapt to modern types of open and drought-stressed habitats.

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References

- Bartish, I.V., Hennekens, S., Aidoud, A., Hennion, F. & Prinzing, A. 2010. Species pools along contemporary environmental gradients represent different levels of diversification. *Journal* of *Biogeography* 37: 2317–2331.
- Bennet, J.A., Lamb, E.G., Hall, J.C., Cardinal-McTeague, W.M. & Cahill, J.F. Jr 2013. Increased competition does not lead to increased phylogenetic overdispersion in a native grassland. *Ecology Letters* 16: 1168–1176.
- Bouchenak-Khelladi, Y., Verboom, G.A., Savolainen, V. & Hodkinson, T.R. 2010. Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society* 162: 543–557.

- Brunbjerg, A.K., Borchsenius, F., Eiserhardt, W.L., Ejrnæs, R. & Svenning, J.-C. 2012. Disturbance drives phylogenetic community structure in coastal dune vegetation. *Journal of Vegetation Science* 23: 1082–1094.
- Butterfield, B.J., Cavieres, L.A., Callaway, R.M., Cook, B.J., Ki-kvidze, Z., Lortie, C.J., Michalet, R., Pugnaire, F.I., Schöb, C., (...) & Brooker, R.W. 2013. Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters* 16: 478–486.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- Chytrý, M. 2012. Vegetation of the Czech Republic: diversity, ecology, history and dynamics. *Preslia* 84: 427–504.
- Coiffard, C., Gomez, B., Daviero-Gomez, V. & Dilcher, D.L. 2012. Rise to dominance of angiosperm pioneers in European Cretaceous environments. *Proceedings of the National Academy of Sciences of the United States of America* 109: 20955–20959.
- Danihelka, J., Chrtek, J. Jr & Kaplan, K. 2012. Checklist of vascular plants of the Czech Republic. *Preslia* 84: 647–811.
- Durka, W. & Michalski, S.G. 2012. DaPhnE: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology* 93: 2297.
- Eastman, J.M., Paine, C.E.T. & Hardy, O.J. 2011. SpacodiR: structuring of phylogenetic diversity in ecological communities. *Bioinformatics* 27: 2437–2438.
- Ellenberg, H. 1988. *Vegetation ecology of Central Europe*. Cambridge University Press, Cambridge, UK.
- Emerson, B.C. & Gillespie, R.G. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution* 23: 619−630.
- Ford, B.A., Iranpour, M., Naczi, R.F.C., Starr, J.R. & Jerome, C.A. 2006. Phylogeny of *Carex* subg. *Vignea* (Cyperaceae) based on non-coding nrDNA sequence data. *Systematic Botany* 31: 70–82.
- Franzke, A., Lysak, M.A., Al-Shehbaz, I.A., Koch, M.A. & Mummenhoff, K. 2011. Cabbage family affairs: the evolutionary history of Brassicaceae. *Trends in Plant Science* 16: 108– 116.
- Gerhold, P., Pärtel, M., Liira, J., Zobel, K. & Prinzing, A. 2008. Phylogenetic structure of local communities predicts the size of the regional species pool. *Journal of Ecology* 96: 709–712.
- Gerhold, P., Cahill, J.F. Jr, Winter, M., Bartish, I.V. & Prinzing, A. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614.
- Gotelli, N.J. & Rohde, K. 2002. Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecology Letters* 5: 86–94.
- Hardy, O.J. 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* 96: 914–926.
- Hardy, O.J. & Senterre, B. 2007. Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology* 95: 493–506.

- Hardy, O.J., Couteron, P., Munoz, F., Ramesh, B.R. & Pélissier, R. 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. *Global Ecology and Biogeography* 21: 1007–1016.
- Hejný, S., Slavík, B., Chrtek, J., Tomšovic, P. & Kovanda, M. (eds.) 1988. Květena České socialistické republiky [Flora of the Czech Socialist Republic], vol 1. Academia, Praha, CZ.
- Kembel, S.W. & Hubbell, S.P. 2006. The phylogenetic structure of a Neotropical forest tree community. *Eωlogy* 87: S86–S99.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- Leibold, M.A., Economo, E.P. & Peres-Neto, P. 2010. Metacommunity phylogenetics separating the roles of environmental filters and historical biogeography. *Ecology Letters* 13: 1290– 1299.
- Lessard, J.-P., Belmaker, J., Myers, J.A., Chase, J.M. & Rahbek, C. 2012. Inferring local ecological processes amid species pool influences. *Trends in Ecology & Evolution* 27: 600–607.
- Letcher, S.G. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society of London, Series B* 277: 97–104.
- Letcher, S.G., Chazdon, R.L., Andrade, A.C.S., Bongers, F., van Breugel, M., Finegan, B., Laurance, S.G., Mesquita, R.C.G., Martínez-Ramos, M. & Williamson, G.B. 2012. Phylogenetic community structure during succession: evidence from three Neotropical forest sites. *Perspectives in Plant Ecology, Evolution* and Systematics 14: 79–87.
- Linder, P.H. & Rudall, P.J. 2005. Evolutionary history of Poales. Annual Review of Ecology, Evolution and Systematics 36: 107– 124.
- Mai, D.H. 1995. Tertiäre Vegetationsgeschichte Europas: Methoden und Ergebnisse. Gustav Fischer, Jena, DE.
- Mayfield, M.M. & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.
- Ozinga, W.A., Schaminée, J.H.J., Bekker, R.M., Bonn, S., Poschlod, P., Tackenberg, O., Bakker, J. & van Groenendael, J.M. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108: 555–561.
- Peres-Neto, P.R., Leibold, M.A. & Dray, S. 2012. Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology* 93: S14–S30.
- Prinzing, A., Reiffers, R., Braakhekke, W.G., Hennekens, S.M., Tackenberg, O., Ozinga, W.A., Schaminée, J.H.J. & van Groenendael, J.M. 2008. Less lineages – more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecology Letters* 11: 809–819.
- Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W., Kühn, I., Winter, M. & Prentice, H.C. 2013. Contrasting changes in taxonomic, phylogenetic and func-

tional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology* 101: 857–866.

- Sádlo, J., Chytrý, M. & Pyšek, P. 2007. Regional species pools of vascular plants in habitats of the Czech Republic. *Preslia* 79: 303–321.
- Schneider, H., Schuettpelz, E., Pryer, K.M., Cranfill, R., Magallón, S. & Lupia, R. 2004. Ferns diversified in the shadow of angiosperms. *Nature* 428: 553–557.
- Schuster, T.M., Setaro, S.D. & Kron, K.A. 2013. Age estimates for the buckwheat family Polygonaceae based on sequence data calibrated by fossils and with a focus on the amphi-Pacific Muehlenbeckia. *PLoS ONE* 8: e61261.
- Shaw, J.A., Devos, N., Cox, C.J., Boles, S.B., Shaw, B., Buchanan, A.M., Cave, L. & Seppelt, R. 2010. Peatmoss (Sphagnum) diversification associated with Miocene Northern Hemisphere climatic cooling? *Molecular Phylogenetics and Evolution* 55: 1139–1145.
- Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M.F., Joseph, J.A. & Dolphin, K. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society of London, Series B* 273: 39–44.
- Stromberg, C.A.E. 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Sciences 39: 517–544.
- Tichý, L. 2002. JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453.
- Valiente-Banuet, A. & Verdú, M. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10: 1029–1036.
- Wang, H., Moore, M.J., Soltis, P.S., Bell, C.D., Brockington, S.F., Alexandre, R., Davis, C.C., Latvis, M., Manchester, S.R. & Soltis, D.E. 2009. Rosid radiation and the rapid rise of angiosperm-dominated forests. *Proceedings of the National Academy* of Sciences of the United States of America 106: 3853–3858.
- Webb, C.O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist* 156: 145–155.
- Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. 2002. Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics* 33: 475–505.

- Webb, C.O., Ackerly, D.D. & Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098–2100.
- Whittaker, R.H. 1975. *Communities and ecosystems*. MacMillan, New York, NY, US.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.-A., (...) & Stephens, P.R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol*ogy Letters 13: 1310–1324.
- Yan, Y., Yang, X. & Tang, Z. 2013. Patterns of species diversity and phylogenetic structure of vascular plants on the Qinghai-Tibetan Plateau. *Ecology and Evolution* 3: 4584– 4595.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology* & *Evolution* 12: 266–269.
- Zobel, M., Otto, R., Laanisto, L., Naranjo-Cigala, A., Pärtel, M. & Fernández-Palacios, J.M. 2011. The formation of species pools: historical habitat abundance affects current local diversity. *Global Ecology and Biogeography* 20: 251–259.
- Zohary, D. 1996. The mode of domestication of the founder crops of southwest Asian agriculture. In: Harris, D.R. (ed.) *The origins and spread of agriculture and pastorism in Eurasia*, pp. 142–158. UCL Press, London, UK.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phylogenetic structure of species pools of 88 plant community types of the Czech Republic.

Appendix S2. Nodes in the phylogeny with significantly more/less daughter taxa in particular species pools.