



**Postglacial colonization of black alder (*Alnus glutinosa*) and grey
alder (*Alnus incana*) in Europe**

Postglaciální kolonizace olše lepkavé (*Alnus glutinosa*) a olše šedé
(*Alnus incana*) v Evropě

Thesis extended summary

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General introduction

Current species distribution in Europe was mainly influenced by massive climatic and environmental changes during the Quaternary period (Hofreiter & Stewart 2009). Alteration of glacials and interglacials caused contractions and expansions of species ranges (Hewitt 1996; Taberlet *et al.* 1998). Last Ice Age, especially the Late Pleniglacial (LPG), was an interval of the most extreme glacial conditions and, by extension, the maximum contraction of tree populations (Tzedakis *et al.* 2013). This interval, which lasted from 15 000 to 24 000 cal. yr BP (Tzedakis *et al.* 2013), certainly had major effect on current distribution of European species (e.g. Bennett *et al.* 1991; Taberlet 1998; Hewitt 1999).

During last few decades, different theories concerning survival of tree species during the LPG period in Europe were proposed (Huntley & Birks 1983; Bennett *et al.* 1991; Frenzel *et al.* 1992; Willis *et al.* 2000; Stewart & Lister 2001; Parducci *et al.* 2012; Tzedakis *et al.* 2013). First concept known as tree-less tundra model or the classical southern refugium theory was based on palaeoecological records and first genetic studies (Huntley & Birks 1983; Bennett *et al.* 1991; Frenzel *et al.* 1992; Hewitt 1996, 1999; Taberlet *et al.* 1998). According to this theory only south of Europe provided topography and climatic conditions suitable for long term survival of many tree species through the climatic cycles (Hewitt 1999; Tzedakis *et al.* 2002). In the contrary, according to second theory, known as concept of cryptic refugia, southern

refugia for animal and plant taxa were supplemented by cryptic refugia in northern parts (Stewart & Lister 2001). Despite the fact that there are many evidences supporting this theory both for boreal and temperate tree species, including plenty direct evidences from fossil and genetic analysis (e.g. Willis & Van Andel 2004; Binney *et al.* 2009; Parducci *et al.* 2012; De Lafontaine *et al.* 2013, 2014), the importance of northern cryptic refugia is still under active debate (Birks *et al.* 2012; Tzedakis *et al.* 2013, Huntley 2014).

Phylogeographic studies have shown that refugia of many European tree species were located in southern European Peninsulas (King & Ferris 1998; Palmé & Vendramin 2002; Grivet & Petit 2003) and the most common migration route was the postglacial colonization from the Balkan Peninsula (King & Ferris 1998; Grivet & Petit 2003; Hampe *et al.* 2003; Cottrell *et al.* 2005; Cornille *et al.* 2013). From genetic data there is nearly no evidence pointing to existence of northern refugia for temperate trees. On the other hand, refugia in northern areas such as northern Carpathians, Russian plains and central Europe were commonly proposed for boreal tree species (Palmé *et al.* 2003a, b; Cheddadi *et al.* 2006; Maliouchenko *et al.* 2007; Tollefsrud *et al.* 2008). Despite previous phylogeographic studies have brought valuable knowledge about postglacial colonization of European tree species, they still have suffered from many limits such as insufficient geographical sampling and using of less variable genetic markers. It was shown that studies which combined different methods, ideally review the fossil data and analyse sufficient number of samples across the whole distribution range by more

molecular markers, can shed a new light on geographical position of glacial refugia and postglacial migration routes (Cheddadi *et al.* 2006; Magri *et al.* 2006). Moreover, using more variable molecular markers such as microsatellites can provide us more detailed picture of postglacial colonization (Heuertz *et al.* 2004b; Tollefsrud *et al.* 2009; Cornille *et al.* 2013).

There are several reasons, why black alder (*Alnus glutinosa*) and grey alder (*Alnus incana*) are suitable species for new phylogeographic study: (1) Studying these two species enable us to compare postglacial histories of temperate tree (*A. glutinosa*) and boreal tree (*A. incana*) which are expected to differ significantly. (2) These two species cannot always be successfully distinguished based on pollen and macrofossil remains (Huntley & Birks 1983). (3) Distributions of both alders have not been largely expanded by human reforestation; thus there are plenty of non-planted stands especially on waterlogged sites. (4) *Alnus* species are keystones of alluvial and wetland habitats (Douda *et al.* 2009; Douda 2010) distributed through the European forest zones from the northern treeline to the Mediterranean, therefore understanding the past history and postglacial migration pattern of *Alnus* populations may help understand the resistance and resilience of wetland forest habitats to global climate change (Erwin 2008; Garssen *et al.* 2015). (5) There are substantial gaps in reconstructions of postglacial histories of *A. glutinosa* and *A. incana* in Europe. It partly results from difficulties with species determination only from fossil records (Huntley & Birks 1983) and partly from the lack of molecular studies.

Aims, questions and hypothesis of dissertation thesis

My dissertation thesis aims to combine information from fossil records and genetic analysis to improve knowledge on locations of glacial refugia and postglacial colonization routes of *Alnus glutinosa* and *Alnus incana*. To find more details, our molecular study will be based on extensive population sampling, will test hypotheses coming from comprehensive fossil analysis and will combine two genetic markers, i.e. chloroplast DNA and microsatellites. Maternally inherited cpDNA will give us coarse picture of individual haplotype distribution all over Europe and recombining genetic marker, i.e. microsatellites, will provide us with precise information concerning population-genetic structure, gene flow among populations, the degree of inbreeding and isolation by distance. Based on the results, important questions concerning the postglacial colonization and changes in genetic pattern of populations during the last glacial cycle in Europe will be able to be answered. The thesis will shed light up on: (i) refugia of *A. glutinosa* and *A. incana* important for postglacial colonization of Europe, (ii) possible existence of northerly located refugia in the proximity of glacier, (iii) postglacial migration routes of both *Alnus* species and (iv) character of colonization, i.e. form of dispersal, gene flow among populations and loss of genetic variation during migration.

Using published data (Tallantire 1974; Huntley & Birks 1983; Chambers & Elliott 1989; Hewitt 1996; King & Ferris 1998; Cruzan & Templeton 2000;

Stewart & Lister 2001; Willis & Van Andel 2004) I formulated a set of specific questions and hypotheses that can be directly tested by empirical data.

Q1: Did *A. glutinosa* and *A. incana* differ in geographic position of their source refugia for postglacial colonization? Did they colonize Europe from single source area or from multiple refugia? More cold-tolerant *A. incana* could be present in the central and eastern European mountain areas and north-west Russia lowlands, whereas southern European peninsulas and lowlands with large rivers in south-west Russia and Ukraine could be the main effective refugia for *A. glutinosa* (H1).

Q2: Did refugia of alders occur in the proximity of glaciers during the LPG; if so, which role did they play during colonization of Europe? Several northern areas such as southeast Great Britain, central Germany, Czech Republic and north-west Russia could be refugia of alders during the LPG (H2).

Q3: Do *A. glutinosa* and *A. incana* differ in their genetic population subdivision? We hypothesize that *A. glutinosa* as the more sensitive species to unfavourable climate will be characterized by higher genetic differentiation than *A. incana* due to its retirement to more isolated southern refugia during the last glaciation (H3).

Q4: What role did the long-distance dispersal events play during colonization of alder species? The coarse patch patterns in genetic subdivision will be apparent, if the rare long-distance dispersal events were important during the colonization process (H4).

Q5: Does genetic variation change with distance to source area of Holocene range expansion? A decrease of genetic variation along with an increasing distance from glacial refugia is expected due to the process of genetic drift following the expansion (H5)

*Migration patterns of subgenus *Alnus* in Europe since the Last Glacial Maximum*

Abstract

Recently, new palaeoecological records supported by molecular analyses and palaeodistributional modelling have provided more comprehensive insights into plant behaviour during the last Quaternary cycle. We reviewed the migration history of species of subgenus *Alnus* during the last 50 000 years in Europe with a focus on (1) a general revision of *Alnus* history since the Last Glacial Maximum (LGM), (2) evidence of northern refugia of *Alnus* populations during the LGM and (3) the specific history of *Alnus* in particular European regions.

We determined changes in *Alnus* distribution on the basis of 811 and 68 radiocarbon-dated pollen and macrofossil sites, respectively. We compiled data from the European Pollen Database, the Czech Quaternary Palynological Database, the Eurasian Macrofossil Database and additional literature. Pollen percentage thresholds indicating expansions or retreats were used to describe patterns of past *Alnus* occurrence.

An expansion of *Alnus* during the Late Glacial and early Holocene periods supports the presence of alders during the LGM in southern peninsulas and northerly areas in western Europe, the foothills of the Alps, the Carpathians and northeastern Europe. After glaciers withdrew, the ice-free area of Europe

was likely colonized from several regional refugia; the deglaciated area of Scandinavia was likely colonized from a single refugium in northeastern Europe. In the more northerly parts of Europe, we found a scale-dependent pattern of *Alnus* expansion characterised by a synchronous increase of *Alnus* within individual regions, though with regional differences in the times of the expansion. In southern peninsulas, the Alps and the Carpathians, by contrast, it seems that *Alnus* expanded differently at individual sites rather than synchronously in whole regions.

Our synthesis supports the idea that northern LGM populations were important sources of postglacial *Alnus* expansion. The delayed *Alnus* expansion apparent in some regions was likely a result of environmental limitations.

Citation: Migration patterns of subgenus *Alnus* in Europe since the Last Glacial Maximum: a systematic review. PloS one, 2014, **9**, e88709.

Autorship: Douda J, Doudová J, Drašnarová A, Kuneš P, Hadincová V, Krak K, Zákavský P, Mandák B

Keywords: colonization, Holocene, Late Glacial period, LGM refugia, plant macrofossil remains, pollen records, regional differences, species expansion, trees

Cross-amplification and multiplexing of SSR markers for *Alnus glutinosa* and *A. incana*

Abstract.

We investigated 39 previously developed *Betula*, *Alnus*, and *Corylus* simple sequence repeat (SSR) markers for their utility in the cross-generic amplification of two European alder species, i.e., *Alnus glutinosa* and *A. incana*. Of these markers, ten loci had successful amplification within *Alnus* species.

Finally, we designed two multiplexes composed of eight and nine loci for *A. glutinosa* and *A. incana*, respectively. Multiplexes were tested on 100 samples from five different populations of each species across Europe. The majority of loci had a relatively high genetic diversity, were in Hardy–Weinberg equilibrium, and showed low error rates and low occurrence of null alleles.

By comparing sequences of source species and both *Alnus* species, we concluded that repeat motifs of five of these ten loci differed from those described for the source species. These differences represent mainly the modifications of the original motifs and affected compound or interrupted repeats as well as pure ones. The repeat motifs of three loci of the two alder species also differed. These mutations could lead to erroneous estimates of allele homology, because alleles with identical lengths will not have the same number of repeat units. Hence, before using microsatellite markers in studies

comparing two or more species, they should be carefully examined and sequenced to ensure that allele homology is really stable and not affected by various inserts that change the sequence.

Citation: Cross-amplification and multiplexing of SSR markers for *Alnus glutinosa* and *A. incana*. *Tree Genetics & Genomes*, 2014, **10**, 865-873.

Authorship: Drašnarová A, Krak K, Vít P, Doudová J, Douda J, Hadincová V, Zákavský P, Mandák B

Keywords: alder, Betulaceae, microsatellites, DNA sequencing

*Putative glacial refugia inferred from the geographic distribution of *Alnus glutinosa* cytotypes in Europe*

Abstract

Polyploidy in plants is an intensively studied topic. In many groups, two or more cytotypes represent separate biological entities with distinct distribution, history and ecology. This paper examines the distribution and origins of cytotypes of *Alnus glutinosa* in Europe, Northern Africa and Western Asia.

Our combined approach involved flow cytometry and microsatellite analysis of twelve loci in 2,200 plants from 209 populations together with species distribution modelling by MIROC and CCSM climatic models to analyse (i) ploidy and genetic variation; (ii) the origin of tetraploid *A. glutinosa*, considering *A. incana* as a putative parent; and (iii) past distribution of the species.

We for the first time report the occurrence of tetraploid populations of *A. glutinosa* in Europe. The distribution of tetraploids is far from random, forming two geographically well delimited clusters located in the Iberian Peninsula and in the Dinaric Alps. Based on microsatellite analysis, both tetraploid clusters are probably of autopolyploid origin with no indication that *A. incana* was involved in their evolutionary history. A projection of the MIROC distribution model into the Last Glacial Maximum (LGM) showed that (i) populations occurring in the Iberian Peninsula and North Africa are likely to

have been interconnected during the LGM, and that (ii) populations occurring in the Dinaric Alps did not exist throughout the last glacial periods and were retreated south into lowland areas of the Balkan Peninsula.

Newly discovered tetraploid populations are situated in the putative main glacial refugia, and neither of them was probably involved in the colonization of Central and Northern Europe after glacial withdrawal. This could mean that neither the Iberian Peninsula nor the western part of the Balkan Peninsula served as effective refugial areas for northward postglacial expansion of *A. glutinosa*.

Citation: Putative glacial refugia inferred from the geographic distribution of *Alnus glutinosa* cytotypes in Europe. *Annals of Botany*, in press.

Authorship: Mandák B, Vít P, Krak K, Trávníček P, Havrdová A, Hadincová V, Zákřavský P, Jarolímová V, Bacles CFE, Douda J

Keywords: *Alnus*, autopolyploidy, cytotype distribution, ecological niche models, flow cytometry, glacial refugia, microsatellites.

*Recent similarity in distribution ranges does not mean a similar postglacial history: a phylogeographical study of the boreal tree species *Alnus incana* based on microsatellite and chloroplast DNA variation*

Abstract

We reconstructed the historical pattern of postglacial biogeographic range expansion of the boreal tree species *Alnus incana* in Europe.

To assess population genetic structure and diversity, we performed a combined analysis of nuclear microsatellite loci and chloroplast DNA sequences (65 populations, 1004 individuals).

Analysis of haplotype and microsatellite diversity revealed that (i) southeastern refugial populations did not spread north and cannot be considered as important source populations for postglacial recolonization of Europe; (ii) eastern populations did not establish Fennoscandian populations; (iii) Northern Europe, i.e. Fennoscandia and Eastern Europe, has no unique genetic cluster, but represents a mix with a predominant cluster typical for Central Europe; and that (iv) colonization of Fennoscandia and Eastern Europe took place from Central Europe and founding Central-European populations most likely in the Alps.

Our findings highlight the importance of an effective refugium in Central Europe located outside classical southern refugia confirming the existence of

northern refugia for boreal trees in Europe. The postglacial range expansion of *A. incana* did not follow the model established for *Picea abies*. Fennoscandian populations are not derived from Eastern-European ones, but from Central-European ones that originated from populations in the Alps.

Citation: Recent similarity in distribution ranges does not mean a similar postglacial history: a phylogeographical study of the boreal tree species *Alnus incana* based on microsatellite and chloroplast DNA variation. *New Phytologist*, submitted.

Autorship: Mandák B, Havrdová A, Krak K, Hadincová V, Vít P, Zákřavský P, Douda J

Keywords: *Alnus*, approximate Bayesian computation, cpDNA, microsatellite, phylogeography, population structure, postglacial migration.

*Higher genetic diversity in recolonized areas than in refugia of *Alnus glutinosa* triggered by continent-wide lineage admixture*

Abstract

Genetic admixture is supposed to be an important trigger of species expansions because it can create the potential for selection of genotypes suitable for new climatic conditions. Up until now, however, no continent-wide population genetic study has performed a detailed reconstruction of admixture events during natural species expansions. To fill this gap, we analysed the postglacial history of *Alnus glutinosa*, a keystone species of European swamp habitats, across its entire distribution range using two molecular markers, cpDNA and nuclear microsatellites.

CpDNA revealed multiple southern refugia located in the Iberian, Apennine, Balkan and Anatolian Peninsulas, Corsica and North Africa. Analysis of microsatellites variation revealed three main directions of postglacial expansion: 1) from the northern part of the Iberian Peninsula to Western and Central Europe and subsequently to the British Isles, 2) from the Apennine Peninsula to the Alps, and 3) from the eastern part of the Balkan Peninsula to the Carpathians followed by expansion towards the Northern European plains. This challenges the classical paradigm that most European populations originated from refugial areas in the Carpathians.

It has been shown that colonizing lineages have met several times and formed secondary contact zones with unexpectedly high population genetic diversity in Central Europe and Scandinavia. On the contrary, limited genetic admixture in southern refugial areas of *A. glutinosa* renders rear-edge populations in the Mediterranean region more vulnerable to extinction due to climate change.

Citation: Higher genetic diversity in recolonized areas than in refugia of *Alnus glutinosa* triggered by continent-wide lineage admixture. *Molecular Ecology*, in press.

Authorship: Havrdová A, Douda J, Krak K, Vít P, Hadincová V, Zákřavský P, Mandák B

Keywords: approximate Bayesian computation, black alder, climate change, ice ages, phylogeography, temperate tree

Souhrn (summary in Czech)

Tento projekt objasnil nejenom, kde byla umístěna glaciální refugia evropských dřevin a která z nich byla efektivní, ale také ukázal, jaké byly hlavní směry postglaciální migrace. Tyto detailní výsledky bylo možné získat díky velkému množství vzorků z celého areálu druhů obou studovaných olší (*Alnus glutinosa* a *A. incana*), testováním hypotéz stanovených na základě fosilních dat pomocí molekulárních analýz a použitím dvou molekulárních markerů lišících se typem přenosu mezi generacemi a jejich proměnlivostí. Tento přístup nám umožnil změnit některé dlouhodobě přetrvávající teorie a přinesl nové poznatky o postglaciální historii evropských dřevin.

Migrace podrodu *Alnus* v Evropě na základě paleoekologických dat (Článek I)

Paleoekologická data ukázala, že glaciální refugia podrodu *Alnus* se nacházela v západní Evropě, severním podhůří Alp, Rumunských Karpatech a v rozlehlých oblastech na severovýchodě Evropy. Refugia na severovýchodě byla navíc podpořena nálezy makrofosílií v Polsku, Bělorusku, Litvě a Lotyšsku. Z jihoevropských refugií paleoekologická data přesvědčivě potvrdila pouze refugium na Pyrenejském poloostrově.

Expanze podrodu *Alnus* v pobaltských zemích a ve Skandinávii začala před 11 až 10 tisíci lety. Chybějící důkazy o výskytu olší ve střední a severozápadní Evropě poukazují na to, že hlavní zdrojové populace pro kolonizaci Skandinávie se nacházely v severovýchodní Evropě. Oproti tomu,

západoevropské populace byly pravděpodobně zdrojem pro opožděnou expanzi na Britské ostrovy před 10 až 8 tisíci lety. V tuto dobu olše expandovaly i v hercynských pohořích a následně ve Francouzském středohoří před 7 a 8 tisíci lety, přičemž původ zdrojových populací není znám. Zatímco v severských oblastech docházelo k nárůstu populací současně napříč regiony, v jižní Evropě se charakter expanze lišil mezi jednotlivými lokalitami.

Hlavním limitem této studie je nemožnost rozlišit od sebe druhy *A. glutinosa* a *A. incana*. Tudíž nemůžeme na základě paleoekologických dat rozhodnout, kterému z těchto druhů náleží nalezené migrační cesty. Makrofosilní nálezy, které by tento problém mohly vyřešit, jsou bohužel velmi vzácné.

Rozšíření a původ cytotypů druhu *Alnus glutinosa* (Článek III)

V této studii jsme poprvé zaznamenali výskyt tetraploidních populací druhu *A. glutinosa* v Evropě. Tyto tetraploidní populace rostou ve dvou geograficky dobře vymezených územích. První z oblastí se nachází na Iberském poloostrově a severu Afriky. Druhá oblast se rozkládá v Dinárských Alpách a na jihozápadě Řecka. Všechny tetraploidní populace jsou pravděpodobně autoployploidního původu a nevykazují známky toho, že by blízké příbuzný druh *A. incana* hrál roli v jejich evoluční historii.

Výskyt tetraploidních jedinců je vázán na oblasti dvou důležitých glaciálních refugií na Iberském a Balkánském poloostrově. Z tohoto důvodu tyto oblasti nemohly sloužit jako efektivní refugia, protože v severnějších částech Evropy rostou pouze diploidní populace. Zdrojové populace pro

postglaciální kolonizaci se tedy mohly nacházet v oblastech s výskytem diploidních populací jako jsou Pyreneje, východ Balkánského poloostrova, Apeniny nebo v severnějších oblastech jako jsou Karpaty, severní podhůří Alp, západní nebo severovýchodní Evropa.

Výsledky modelování ekologických nik a Bayesiánských analýz mikrosatelitů ukazují, že oblasti s výskytem tetraploidních populací se liší svojí historií. Zatímco populace na Iberském poloostrově pravděpodobně dlouhodobě přežívaly na stejných lokalitách, Balkánské populace jsou spíše výsledkem postglaciální migrace.

Postglaciální historie druhu *Alnus incana* v Evropě (Článek IV)

Konzervativnější chloroplastová DNA ukázala, že haplotypy v jihovýchodní Evropě jsou vzájemně rozrůzněné a liší se od haplotypů ve zbývajících částech Evropy. Postglaciální kolonizace boreálního druhu *A. incana* se pravděpodobně lišila od scénářů navržených pro jiné boreální dřeviny. Většina evropských populací druhu *A. incana* byla totiž kolonizována spíše z jižněji položených oblastí než ze severovýchodní Evropy.

Na základě analýzy mikrosatelitů usuzujeme, že populace v Sudetských pohořích, na západě Karpat a východě Alp pocházejí z kryptického refugia, které se nacházelo ve středoevropských nížinách a pravděpodobně také v nižších polohách horských oblastí s příznivým mikroklimatem. Kryptické refugium ve střední Evropě bylo zdrojem pro postglaciální kolonizaci severní Evropy a je důkazem, že refugia boreálních dřevin se vyskytovala i v severněji položených oblastech Evropy. Oproti tomu populace, které přežívaly poslední

glaciál v jihovýchodní Evropě, nepřispěly ke kolonizaci střední a severní Evropy.

Postglaciální historie druhu *Alnus glutinosa* v Evropě (Článek V)

Chloroplastová DNA rozlišila několik vysoce rozrůzněných haploskupin a vysokou haplotypovou diverzitu v jižních oblastech. To poukazuje na výskyt refugií na Iberském, Apeninském a Balkánském poloostrově, na Korsice, v severní Africe a na Anatólském poloostrově. Kromě toho jsme objevili důkaz pro existenci severněji položeného refugia v Karpatech, kde jsme objevili unikátní haploskupinu.

Analýza mikrosatelitů nám poskytla detailnější informace o průběhu postglaciální kolonizace než chloroplastová DNA. Ukázalo se, že všechna tři jihoevropská refugia přispěla k postglaciální kolonizaci Evropy. ABC analýza, která proti sobě testovala více možných scénářů, vybrala nejpravděpodobnější cesty postglaciální kolonizace: 1) z Iberského poloostrova do střední a západní Evropy a následně na Britské ostrovy, 2) z Apeninského poloostrova do Alp a 3) z Balkánského poloostrova do Karpat a následně do severní Evropy. V průběhu kolonizace vznikly dvě sekundární kontaktní zóny: (i) migrační proudy ze západní Evropy a z Karpat se setkaly ve střední Evropě a (ii) skandinávské populace jsou tvořeny západoevropskými a východoevropskými populacemi. Setkávání různých linií v průběhu postglaciální kolonizace se zdá být hlavním důvodem vysoké genetické diverzity i mimo refugiální oblasti.

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2011–2014: GAČR project: Postglacial colonization of *Alnus glutinosa* and *Alnus incana*: analysis of DNA variation and fossil records (P504/11/0402)

2012–2014: CIGA ČZU project: The importance of regional and local processes for plant species diversity in floodplain forests in Europe (20124201)

Conferences

Molecular Ecology Vídeň, 2011: poster Analysis of DNA variation and fossil records in *Alnus glutinosa* and *A. incana*: changes in distribution ranges over time

European Vegetation Survey Vídeň, 2012: poster How is soil seed bank related to topography and succession on alluvial wet meadows?

INTECOL Londýn, 2013: poster Role of regional and local processes for species diversity in floodplain forests of Europe

European Vegetation Survey Ljubljana, 2014: poster Formalized classification of floodplain forests, alder carrs and willow scrubs in Europe

Botany Boise, USA, 2014: posters Analysis of DNA variation and fossil records in *Alnus glutinosa* and *A. incana*: changes in distribution ranges over time and Geographic distribution and the origin of the two cytotypes of *Alnus glutinosa* in Europe

Publication activity

Papers in scientific journals with impact factors

Havrdová A, Douda J, Doudová J (submitted, *Flora*) Local topography affects seed bank successional patterns in alluvial meadows.

Mandák B, **Havrdová A**, Krak K, Hadincová V, Vít P, Zákavský P, Douda J (submitted, *New Phytologist*) Recent similarity in distribution ranges does not mean a similar postglacial history: a phylogeographical study of the boreal tree species *Alnus incana* based on microsatellite and chloroplast DNA variation.

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Douda J, Doudová-Kochánková J, Boublík K, **Drašnarová A** (2012) Plant species coexistence at local scale in temperate swamp forest: test of habitat heterogeneity hypothesis. *Oecologia*, **169**, 523–534.

Papers in other scientific journals

Douda J, **Havrdová A**, Mandák B (in press) Co nám říkají molekulární data o glaciálních refugiích středoevropských dřevin? Zprávy české botanické společnosti.