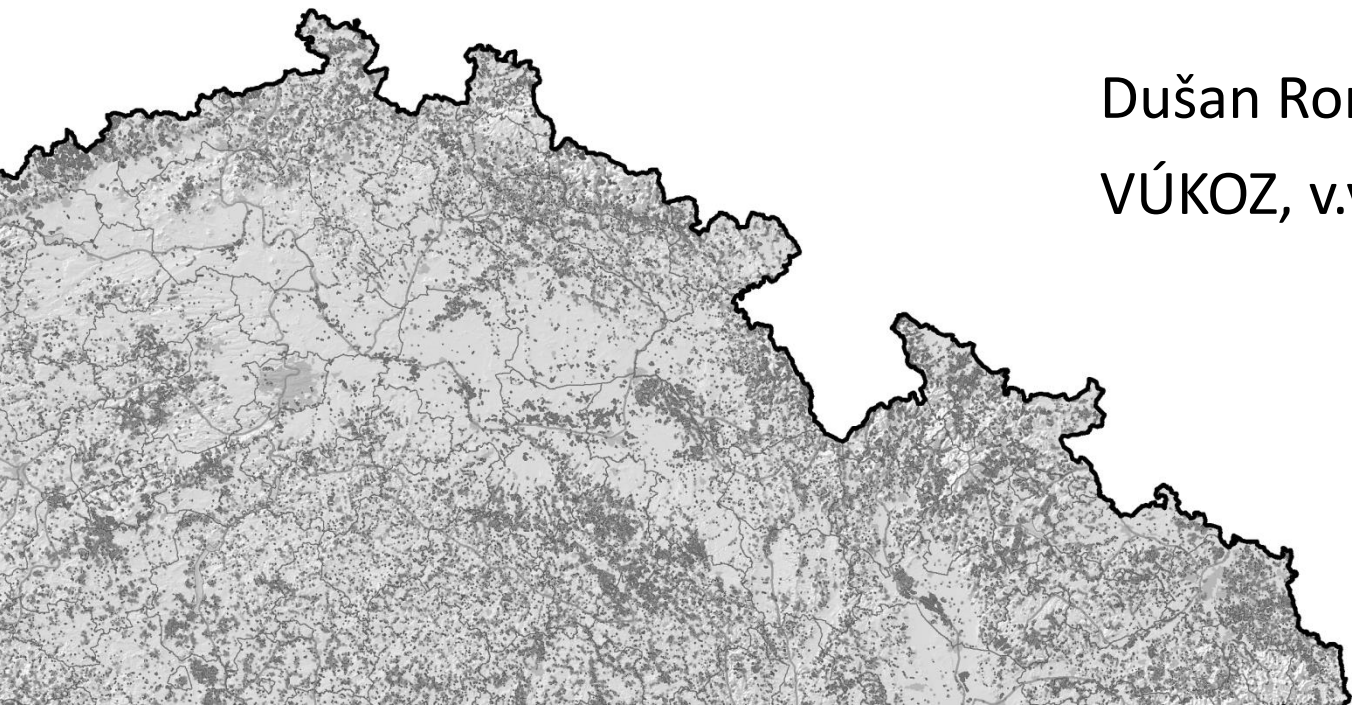
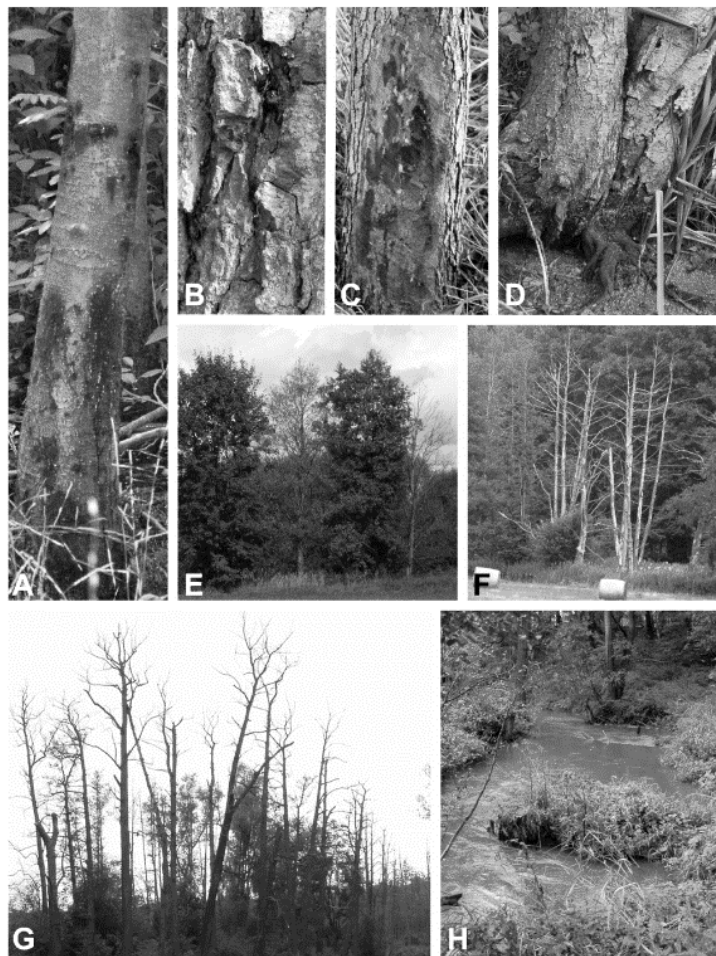


Mapování výskytu fytopatogenů a modelování škod na dřevinách v lesích ČR

Dušan Romportl, Eva Chumanová & Karel Černý
VÚKOZ, v.v.i.



Mapování výskytu vybraných fytopatogenů



Introdukce nepůvodních patogenů dřevin

- zásadní problém lesnictví, ochrany přírody a krajiny a hospodaření v krajině vůbec
- významné ekonomické škody, často nevratné

Mapování

- často obtížná detekce v terénu v počátečním stadiu
- neznámý rozsah výskytu a trajektorie šíření
- nejasné ekologické nároky a limitující faktory

Mapování výskytu vybraných fytopatogenů

Plíseň olšová (*Phytophthora alni*)

- typický nepůvodní invazní organismus
- **oligofág olší** – hniloba kořenů a krčků, poškození dřevin, chřadnutí až odumření
- **transformer** - poškozovány mokřadní aj. olšiny a břehové porosty

Rozsah škod

1. ***vodohospodářství***: poškozeno až 80–90 (–100) % olší v porostu, ekonomické škody, změna struktury břehových porostů, stabilita břehů atd.
2. ***ochrana přírody a krajiny***: nevratné poškození BP, mokřadních olšin, olšin olše šedé, aj.
3. ***lesnictví*** (1,6%, tj. cca 2,6 mil. ha)
4. ***školkařství***

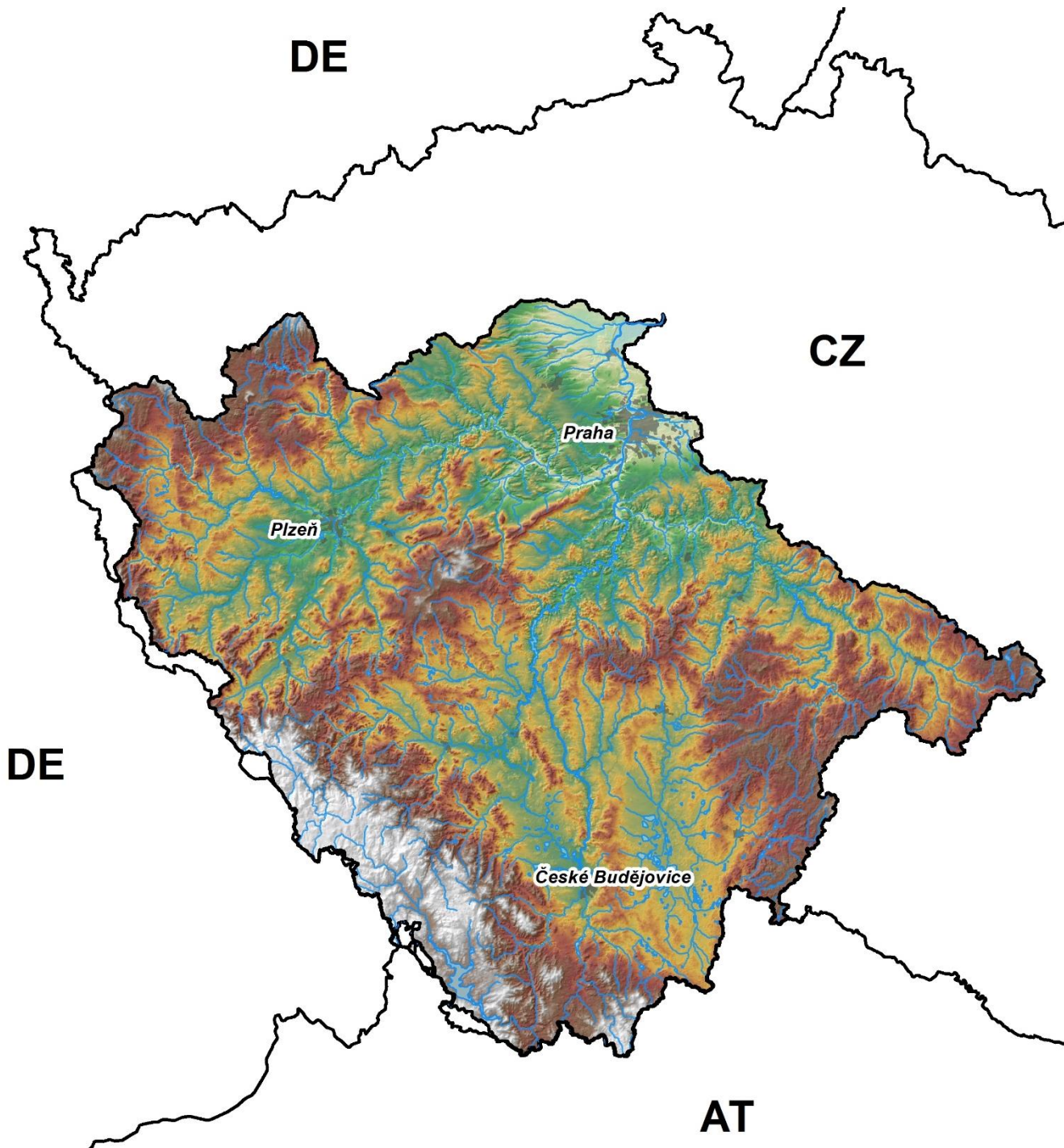
Mapování výskytu vybraných fytopatogenů

Plíseň olšová (*Phytophthora alni*) v ČR

- 1993 - chřadnutí olší: (Jančařík, 1993)
- 2001 - první izolačně doložený výskyt (PA)
- **2002** - souvislost mezi intenzitou poškození a povodněmi
 - PVL: sanace několika desítek tis. olší
- **2010** - více než 400 lokalit
 - tisíce km břehových porostů
 - **invaze mimo kontrolu**
 - největší škody PVL, POH, méně PLA, PMO
 - šíření na východ povodím Moravy
 - úzká vazba na vodní toky, *napadení lesních porostů nepříliš významné*
- **od r. 2001**
 - systematické studium: distribuce, význam, populační analýza, ekologie, epidemiologie, rezistence, možnosti ochrany
 - **nejvíce prostudovaný patogen dřevin**

ČR

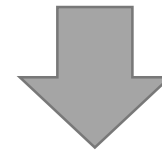
- 1993: chřadnutí olší: JH (Jančařík, 1993)... *PU?*
- 2001: první izolačně doložený výskyt (*PA*)
- 2002:
 - souvislost mezi intenzitou poškození a povodněmi
 - PVL: sanace několika desítek tis. olší
- 2010:
 - více než 400 lokalit
 - tisíce km břehových porostů
 - invaze mimo kontrolu
 - největší škody PVL, POH, méně PLA, PMO
 - šíření na východ povodím Moravy
 - úzká vazba na vodní toky, napadení lesních porostů nepříliš významné



Modelová studie -

Mapování výskytu plísně olšové
(*Phytophthora alni*) v povodí Vltavy

- snaha postihnout všechny typy stanovišť
- zachycení výškového gradientu i míry antropogenní přeměny krajiny
- zhodnocení různého stupně konektivity porostů



- vytvoření **typologie krajiny**
 - stanovení prostorového rámce pro terénní mapování

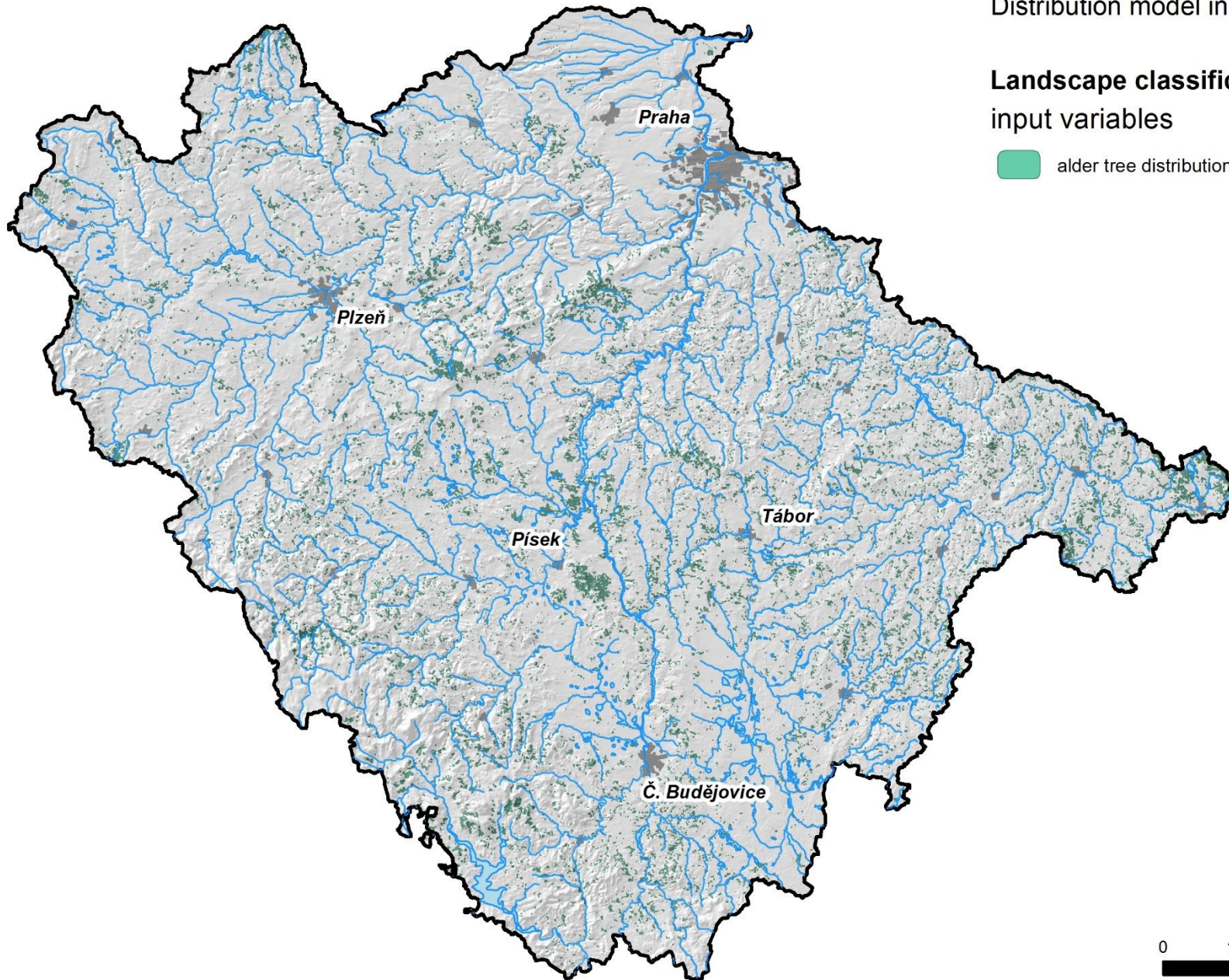
Phytophthora alni

Distribution model in the Vltava watershed

Landscape classification

input variables

 alder tree distribution



0 15 30 60 km

Modelová studie

Design mapování

- stratifikovaný výběr na základě výsledků typologie krajiny

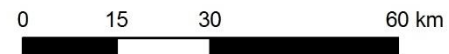
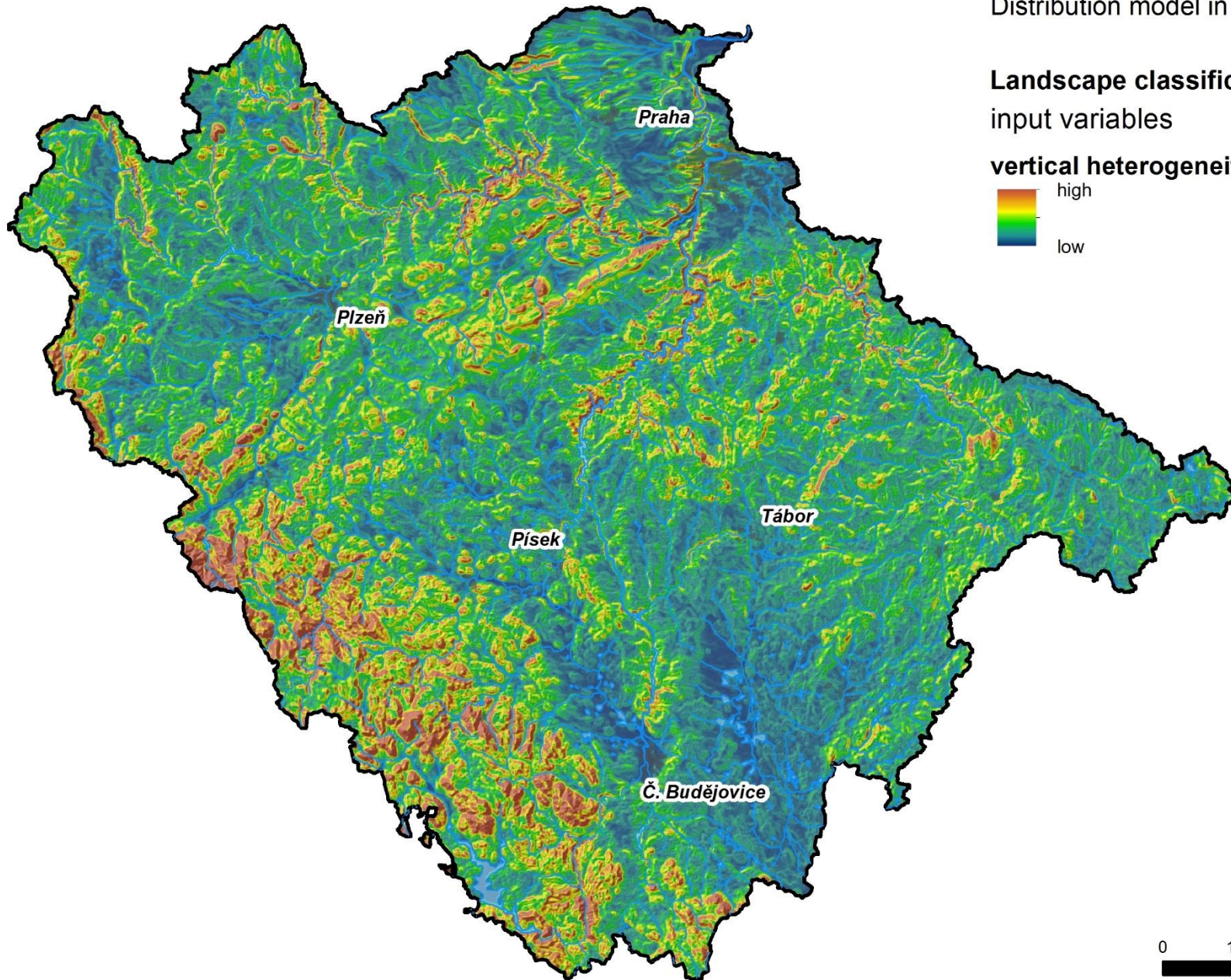
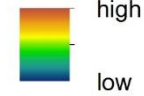
Phytophthora alni

Distribution model in the Vltava watershed

Landscape classification

input variables

vertical heterogeneity



Modelová studie

Design mapování

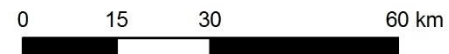
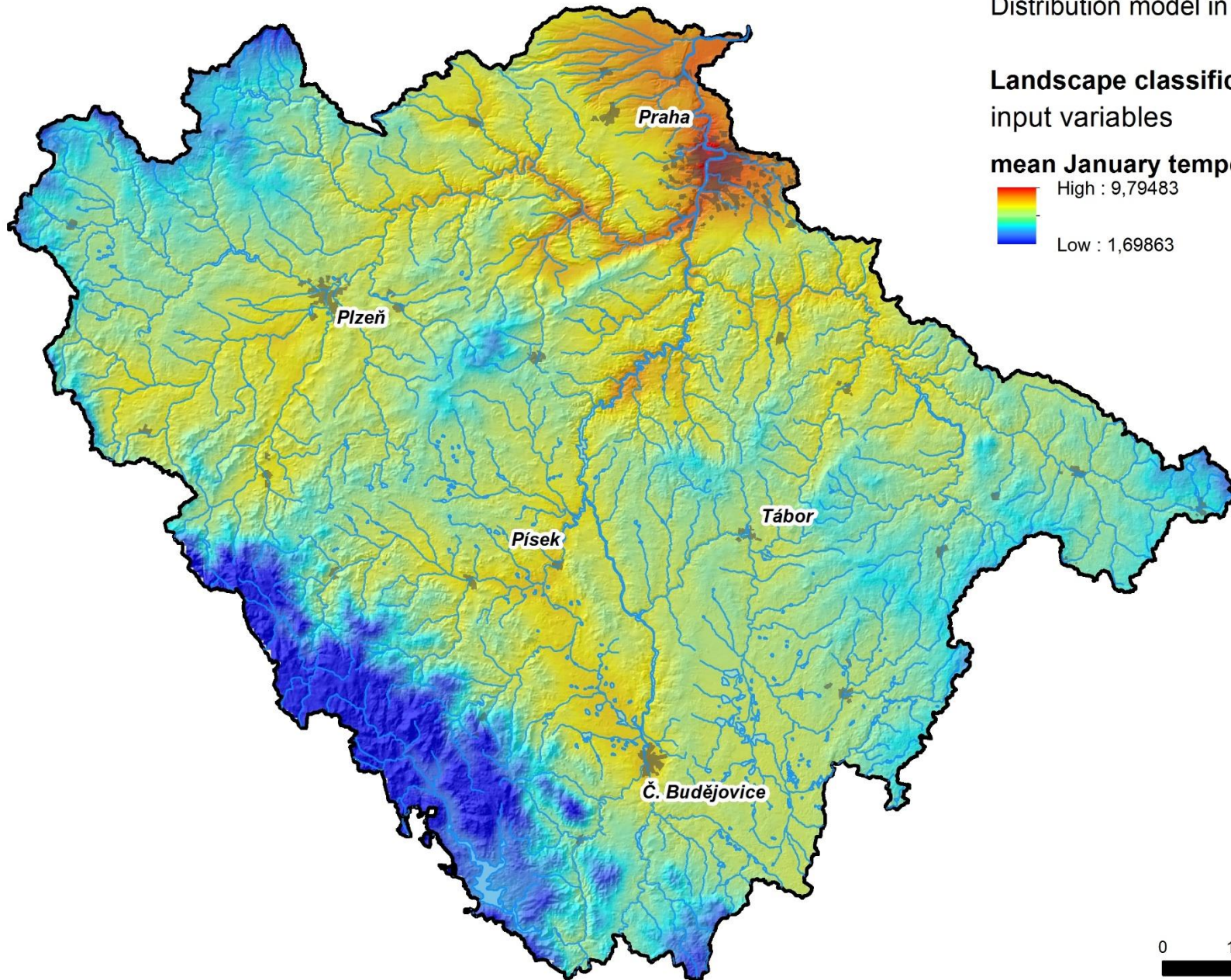
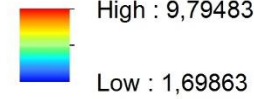
- stratifikovaný výběr na základě výsledků typologie krajiny

Phytophthora alni

Distribution model in the Vltava watershed

Landscape classification
input variables

mean January temperature



Modelová studie

Design mapování

- stratifikovaný výběr na základě výsledků typologie krajiny

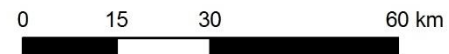
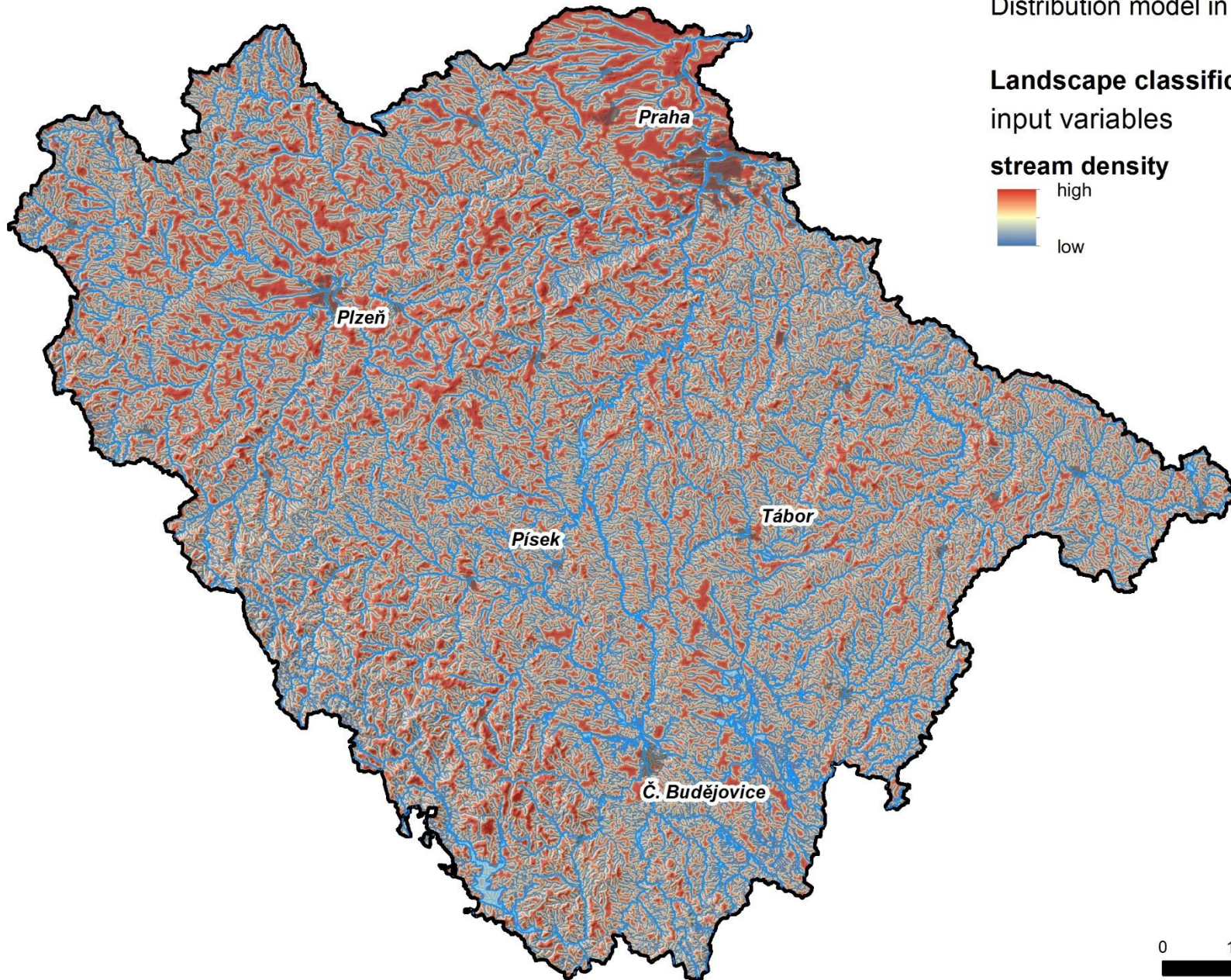
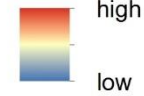
Phytophthora alni

Distribution model in the Vltava watershed

Landscape classification

input variables

stream density



Modelová studie

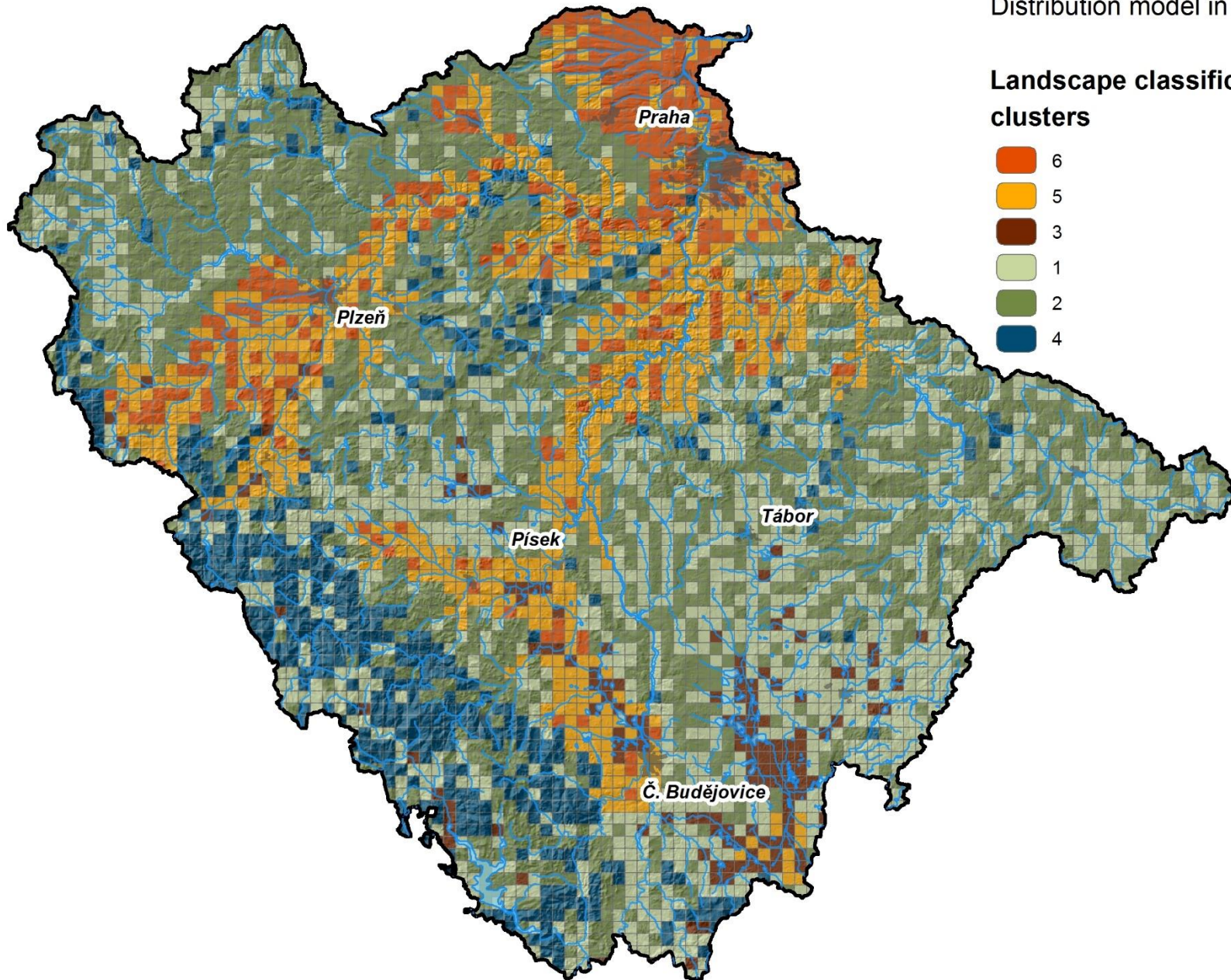
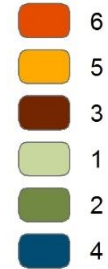
Design mapování

- stratifikovaný výběr na základě výsledků typologie krajiny

Phytophthora alni

Distribution model in the Vltava watershed

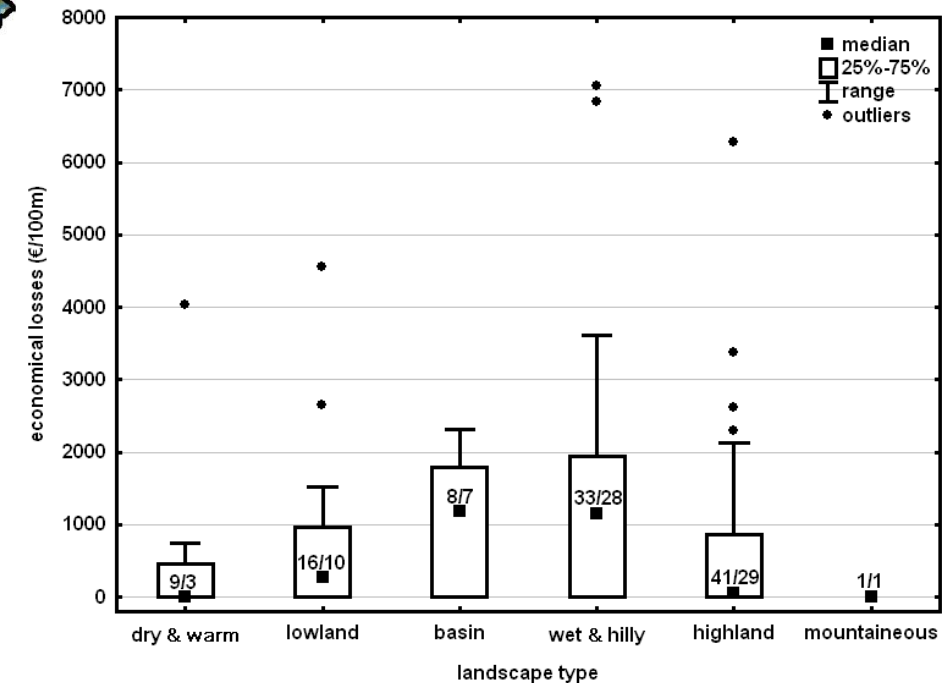
Landscape classification clusters



Modelová studie

Design mapování

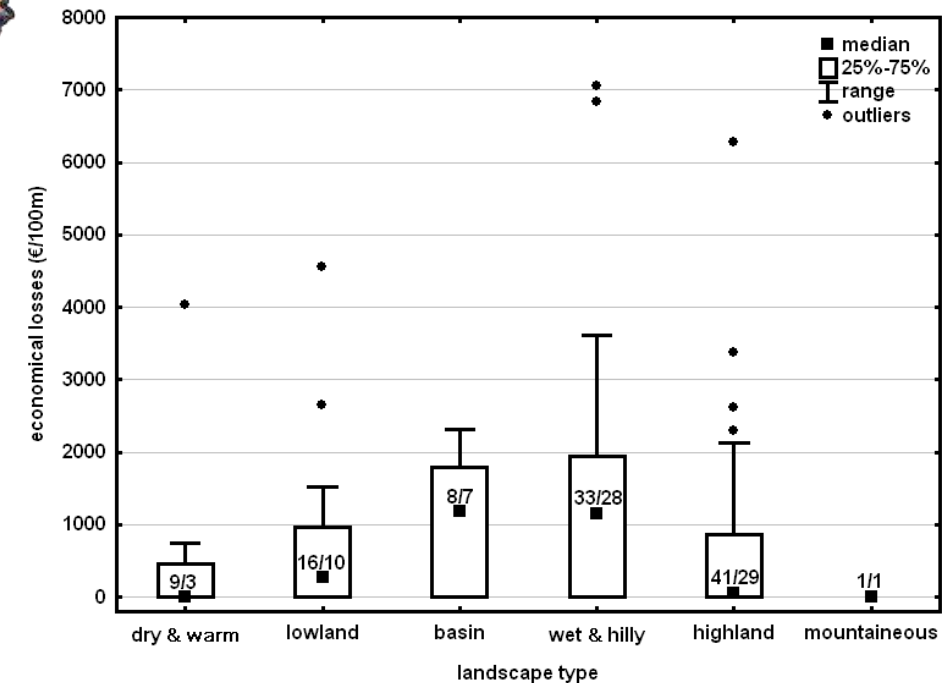
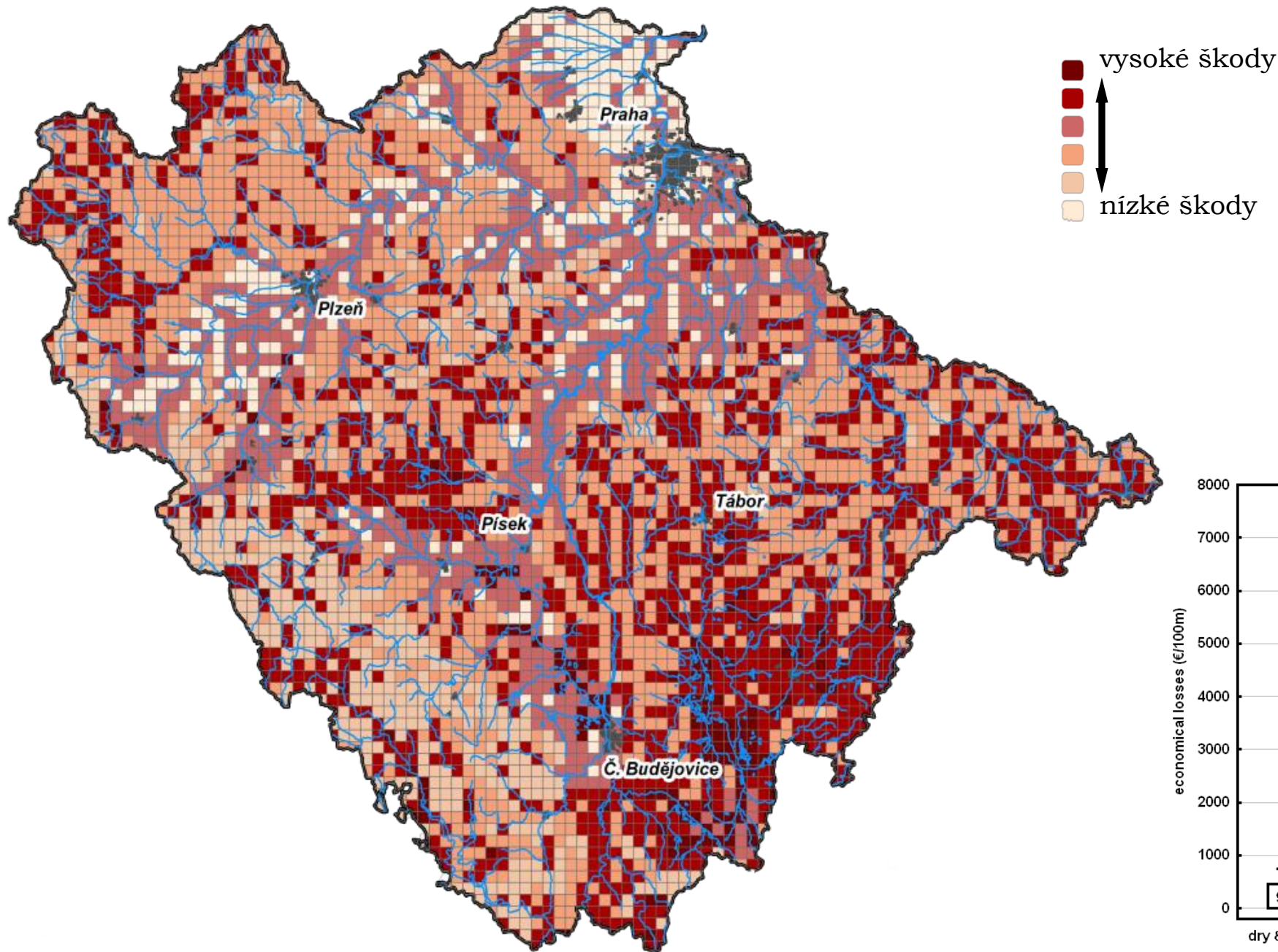
- stratifikovaný
výběr na základě
výsledků
typologie krajiny



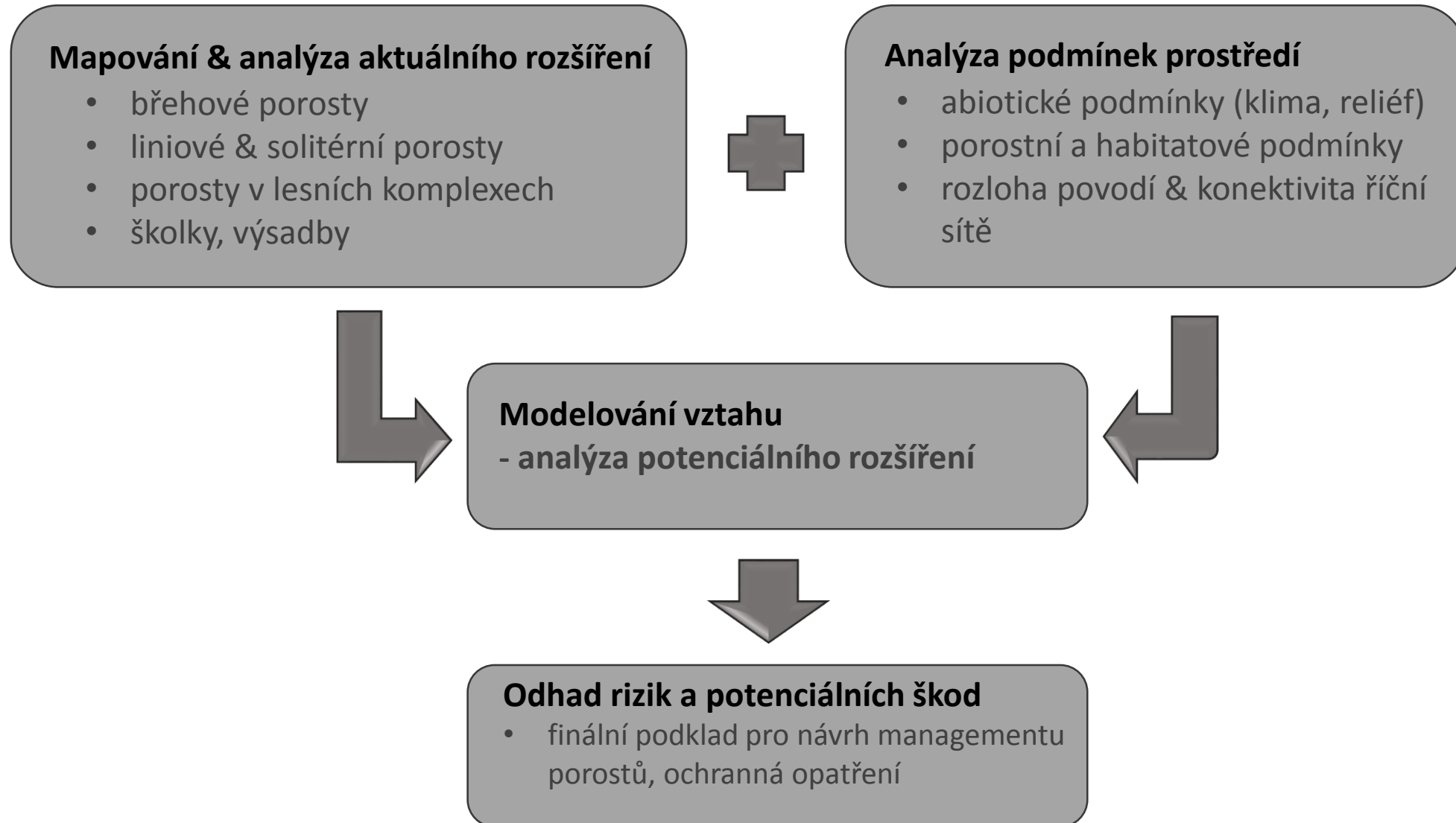
Modelová studie

Design mapování

- stratifikovaný výběr na základě výsledků typologie krajiny



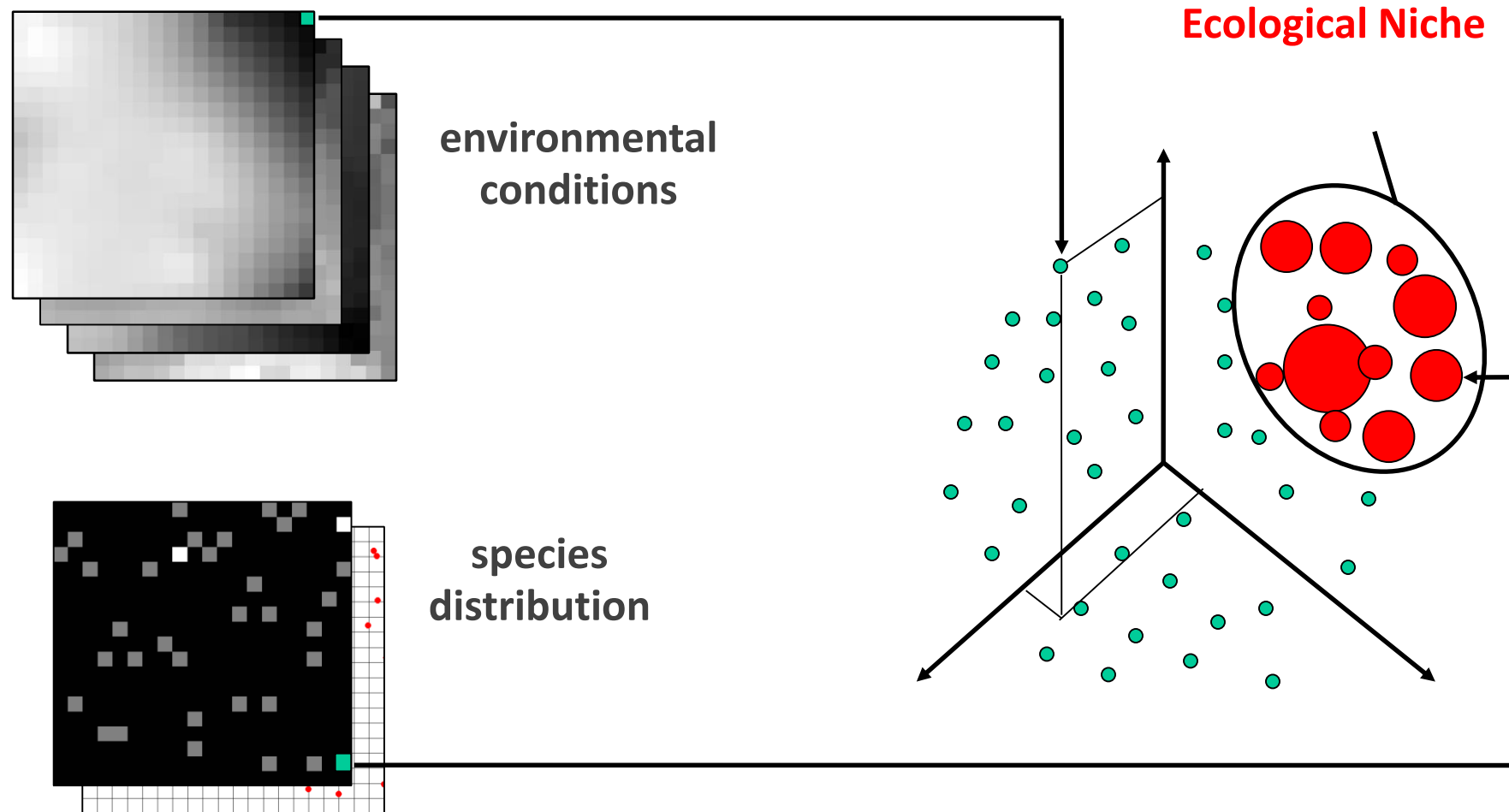
Model výskytu pro celou ČR - metodický postup



Modelování potenciálního výskytu

Maximum Entropy Modelling

- hodnocení vztahu distribuce zájmových druhů k relevantním faktorům prostředí



Model potenciálního výskytu a škod P. alni

Vstupní proměnné

1. ÚROVEŇ POROSTU:

nadmořská výška porostu
lesní vegetační stupeň
skupina lesních typů
přítomnost toku - 1: ne, 2: ano
1: bez toku, 2: do 1 m, 3: do 10 m, 4: nad 10 m
věk porostu
zakmenění
podíl olší na druhové skladbě
výměra porostu
zásoba biomasy
zásoba biomasy v m ³ /ha
prosychání - 1: ne, 2: ano
míra prosychání - 1: ne, 2: <10%, 3: 10-25%, 4: 25-50%, 5: >50%
přítomnost P.alni - 1: ne, 2: ano
kvantifikace PA - 0: není, 1: <10ks, 2: <50 ks, 3: <100 ks, 4: >100 ks

Model potenciálního výskytu a škod P. alni

Vstupní proměnné

2. ÚROVEŇ OKOLÍ POROSTU (BUFFER 500m):

rozloha olšin v okolí
součin rozlohy olšin v okolí a jejich procent. zastoupení v porostu
délka okrajů porostů s olšinami v okolí
podíl lesních ploch v okolí
délka liniové vegetace v okolí
průměrná nadm. výška okolí
vertikální heterogenita reliéfu (std) okolí
průměrná roční teplota v okolí
průměrná lednová teplota v okolí
průměrné roční srážky v okolí

Model potenciálního výskytu a škod P. alni

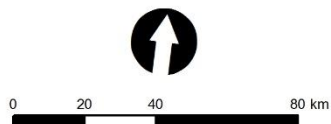
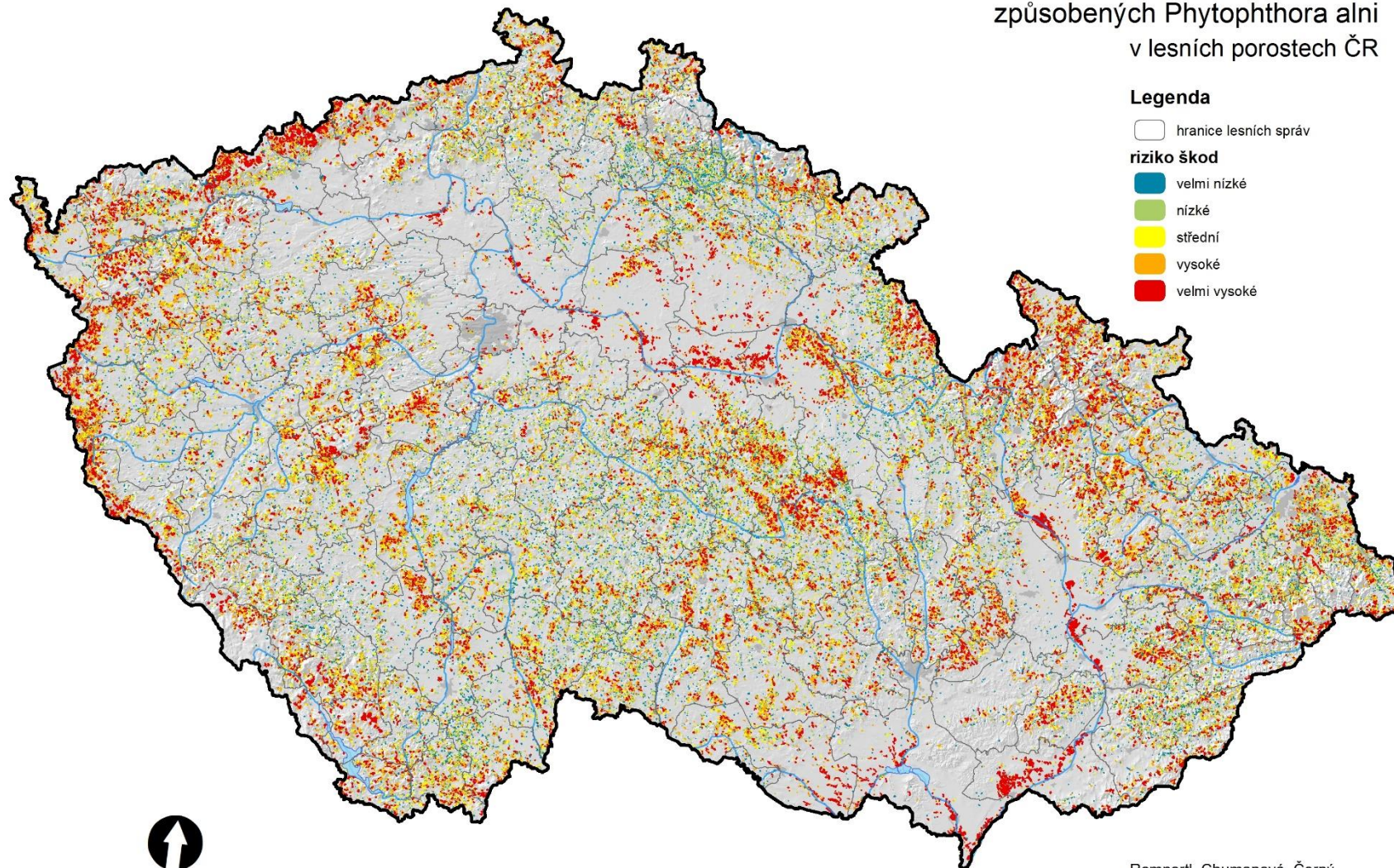
Vstupní proměnné

3. ÚROVEŇ SUMÁRNÍCH POVODÍ:

plocha sumárního povodí
počet porostů olšin v povodí
souhrnná plocha porostů olšin v povodí
součin rozlohy olšin v povodí a jejich procent. zastoupení v porostu
souhrnná délka vodních toků v povodí
počet rybníků v povodí
vertikální heterogenita reliéfu (std) v povodí
podíl zalesněné plochy v povodí

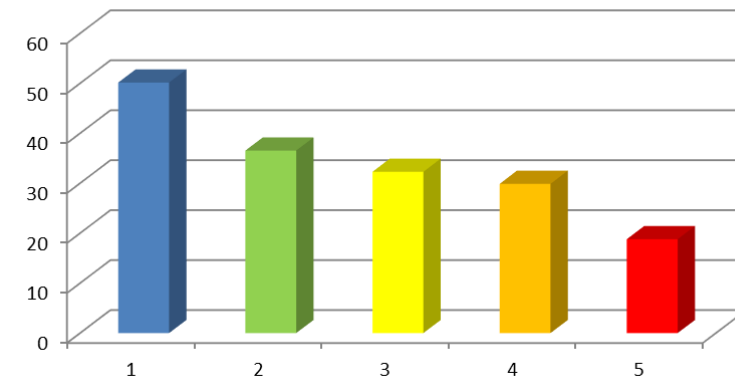
Výsledky modelu

Mapa potenciálního rizika výskytu a škod
způsobených *Phytophthora alni*
v lesních porostech ČR

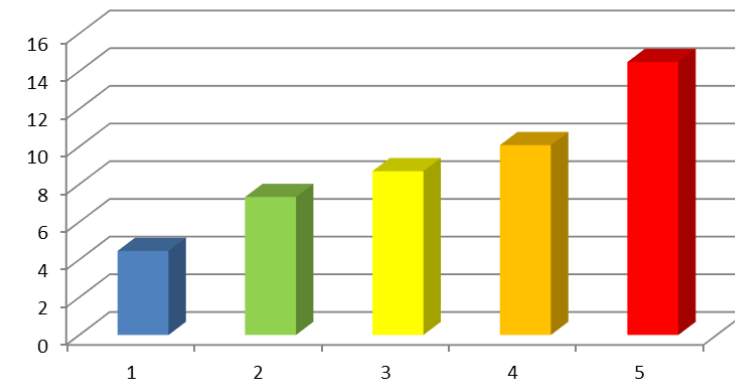


Romportl, Chumanová, Černý,
Havrdová, Pešková, Strnadová
VÚKOZ, v.v.i., 2015

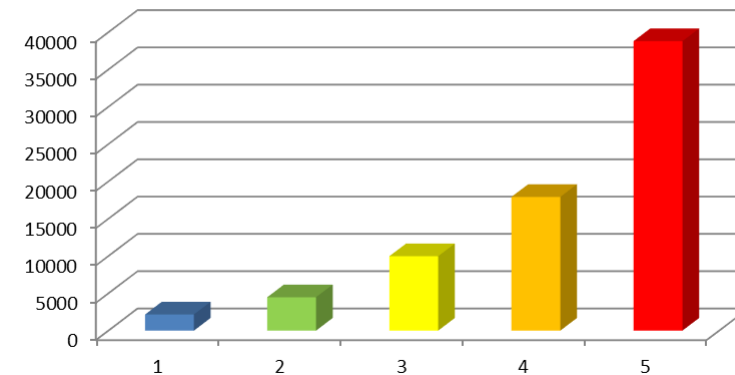
zastoupení olší v porostu (%)



výměra olšin v okolí (ha)



výměra porostu (m2)



Další kroky - modelování šíření

Dispersal model:

CIRCUITSCAPE – THEORY (McRae 2006, McRae et al. 2008)

Evolution, 60(8), 2006, pp. 1551–1561

ISOLATION BY RESISTANCE

BRAD H. McRAE

National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California 93101-5504
E-mail: mcræ@nceas.ucsb.edu



CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecology, 89(10), 2008, pp. 2712–2724
© 2008 by the Ecological Society of America

USING CIRCUIT THEORY TO MODEL CONNECTIVITY IN ECOLOGY, EVOLUTION, AND CONSERVATION

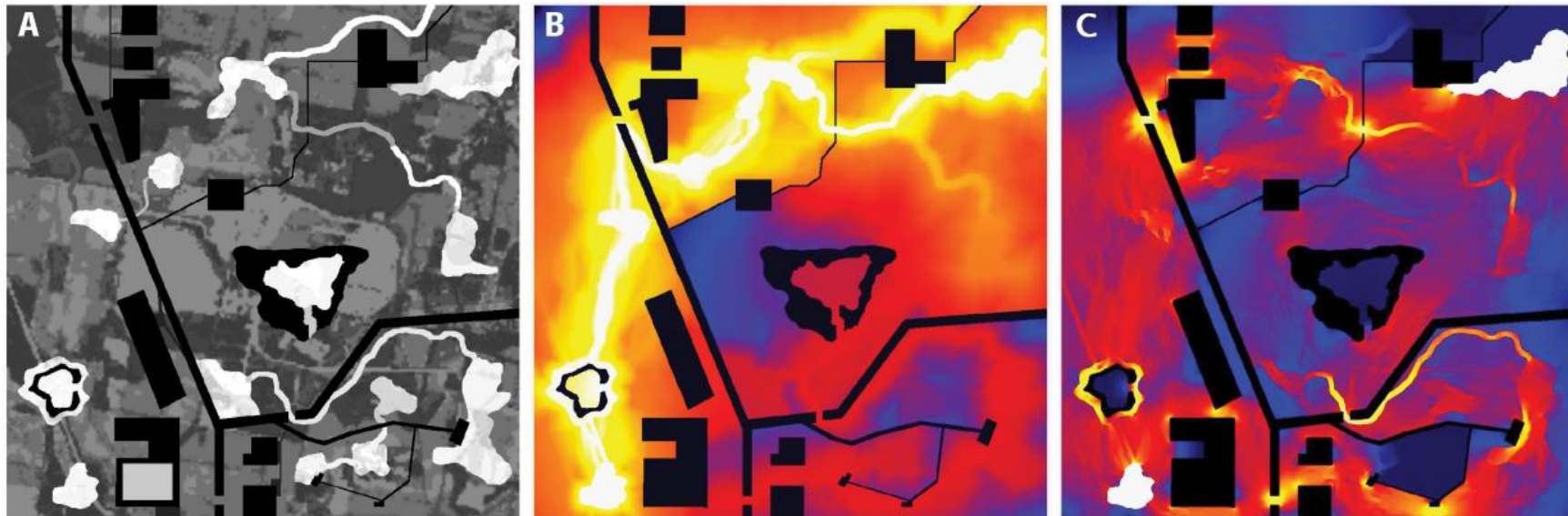
BRAD H. McRAE,^{1,5} BRETT G. DICKSON,² TIMOTHY H. KEITT,³ AND VIRAL B. SHAH⁴

¹National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101 USA

²Center for Environmental Sciences and Education, Northern Arizona University, Flagstaff, Arizona 86011 USA

³Section of Integrative Biology, University of Texas at Austin, Austin, Texas 78712 USA

⁴Department of Computer Science, University of California, Santa Barbara, California 93106 USA



Phytophthora Alder Decline: Disease Symptoms, Causal Agent and Its Distribution in the Czech Republic

KAREL ČERNÝ and VERONIKA ŠTRNADOVÁ

Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Práhonice, Czech Republic

Abstract

ČERNÝ K., ŠTRNADOVÁ V. (2010): *Phytophthora alder* decline: disease symptoms, causal agent and its distribution in the Czech Republic. Plant Protect. Sci., 46: 12–18.*Phytophthora* decline of riparian alder populations has recently become an important problem in many European countries, including the Czech Republic. The causal agent, *Phytophthora alni*, has spread quickly in the Czech

Identification of *Phytophthora alni* Subspecies in Riparian Stands in the Czech Republic

PETRA ŠTĚPÁNKOVÁ¹, KAREL ČERNÝ^{2,3}, VERONIKA ŠTRNADOVÁ², PAVEL HANÁČEK² and MICHAL TOMŠOVSKÝ⁴¹Faculty of Agronomy, Mendel University in Brno, Brno, Czech Republic; ²Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Práhonice, Czech Republic;³Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic; ⁴Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

Abstract

The winter survival of the invasive pathogen *Phytophthora alni* subsp. *alni* in black alder stems was studied in the landscape at the end of the growing period in southern Bohemia at three different sites.

Winter survival of *Phytophthora alni* subsp. *alni* in aerial tissues of black alder

K. ČERNÝ^{1,2}, V. ŠTRNADOVÁ¹¹Department of Biological Risks, Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Práhonice, Czech Republic²Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Prague, Czech RepublicABSTRACT: The winter survival of the invasive pathogen *Phytophthora alni* subsp. *alni* in black alder stems was studied in the landscape at the end of the growing period in southern Bohemia at three different sites.

Key

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The effects of flooding and *Phytophthora alni* infection on black alder

V. ŠTRNADOVÁ, K. ČERNÝ, V. HOUB, B. GREGOROVÁ

Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Práhonice, Czech Republic

ABSTRACT: The influences of long-term flooding and *Phytophthora alni* subsp. *alni* infection on the growth and development of 6-year-old *Alnus glutinosa* (black alder) saplings were investigated. The black alder saplings were divided into four groups and then subjected to combinations of both factors – flooded and inoculated with pathogen, flooded non-inoculated, non-flooded inoculated, and control. The biomass of the living roots and actinorhizas, increase in

Factors affecting the development of *Phytophthora alni* ssp. *alni* infections in *Alnus glutinosa* L.

P. ŠTOCHLOVÁ¹, K. NOVOTNÁ¹, K. ČERNÝ^{1,2}¹Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Práhonice, Czech Republic²Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech RepublicABSTRACT: *Phytophthora alni* is responsible for a devastating disease in alder and changes in the environment of

VÝZKUMNÝ ÚSTAV SILVA TAROUČY
PRO KRAJINU A OKRASNÉ ZAHRADNICTVÍ, v.v.i.
Květnové náměstí 391
Práhonice, PSČ 252 43
Česká republika

Onemocnění olší způsobené druhem *Phytophthora alni* Brasier & S.A. Kirk

Management
napadených
porostů



Influence of low temperature and frost duration on *Phytophthora alni* subsp. *alni* viability

K. ČERNÝ^{1,2}*, N. Filipová^{1,2} and V. Štrnadová¹¹Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Publ. Res. Inst., Práhonice 25243, Czech Republic²Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague 16521, Czech Republic

Abstract

Limits on the survival of *P. alni* subsp. *alni* (PAA) due to low temperature can be expected based on previously published laboratory and field studies. This study presents a laboratory experiment to test the influence of low temperature and frost duration on PAA viability. Ten PAA isolates were incubated at different temperatures (−0.1, −2.5, −5.0, −7.5, and −10.0 °C) and frost durations (0 – 7, 14, 21, and 28 days). A regression analysis confirmed the significant influence of both factors (low temperature and frost duration, and their interaction) on the survival of the pathogen under laboratory conditions. The survival and failure time analysis showed that the survival of the pathogen differs significantly after mild frost (all the isolates tested survived temperatures between −0.1 and −5.0 °C during the entire testing period) and heavy frost (the pathogen died after 21 days of incubation at −7.5 °C and after 2 days at −10.0 °C). Moreover, the viability of the pathogen decreased significantly if the temperature of −5.0 °C was maintained for at least 1 week and the temperature of −7.5 °C persisted in laboratory conditions for at least 4 days. The results of the study proved the pathogen to be very sensitive to heavy frost. The low-temperature limits for PAA occur regularly in Central Europe in January. It is probable that these temperatures can reduce PAA populations in diseased black alder stems. The climate change characterized by increases in the lowest minimum winter temperatures in Central Europe (as hypothesized by IPCC) may pose a significant risk for affected alder population in the area.Key words: *Phytophthora alder* disease; winter survival; viability; temperature; frost.

Resumen

Influencia de las bajas temperaturas y la

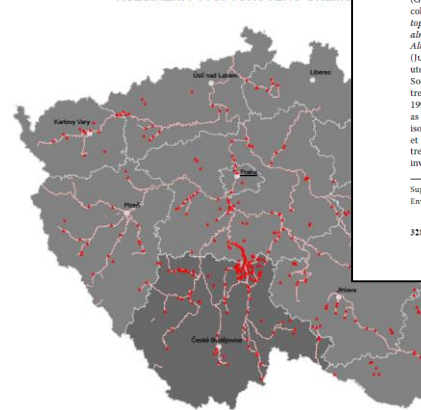
Se pueden esperar límites a la supervivencia de las bajas temperaturas y la duración de las heladas en los resultados obtenidos en laboratorio y para probar la influencia de las bajas temperaturas y la duración de las heladas en la viabilidad de las esporas de PAA a diferentes temperaturas y 28 días). Un análisis de regresión confirmó la influencia significativa de ambos factores (bajas temperaturas y duración de las heladas, y su interacción) sobre la supervivencia y el análisis de tiempo de fallo de las esporas de PAA en condiciones de laboratorio. El análisis de supervivencia y el análisis de tiempo de fallo mostraron que la supervivencia del patógeno difiere significativamente después de una helada leve (todas las esporas sobrevivieron a temperaturas entre −0.1 y −5.0 °C durante todo el período completo de la prueba) y heladas fuertes (el patógeno murió después de 21 días de incubación a −7.5 °C y después de 2 días a −10.0 °C). Además, la viabilidad del patógeno disminuyó significativamente si la temperatura de −5.0 °C se mantuvo durante al menos 1 semana y la temperatura de −7.5 °C persistió en condiciones de laboratorio durante al menos 4 días. Los resultados del estudio muestran que el patógeno es muy sensible a las heladas fuertes. Los límites de baja temperatura para PAA ocurren regularmente en Europa Central en enero. Es probable que estas temperaturas puedan reducir las poblaciones de PAA en los árboles enfermos de álamo negro. Los cambios climáticos caracterizados por un aumento en las temperaturas mínimas invernales más bajas del invierno en Europa Central (según se hipotetiza por el IPCC) pueden representar un riesgo significativo para la población afectada de álamos.

Palabras clave: *Phytophthora* de álamos;

* Corresponding author: černy@vumop.cz

Received: 08-10-11. Accepted: 01-06-12.

ROZŠÍŘENÍ PHYTOFTOROVÉHO ONEMOCNĚNÍ OLŠE



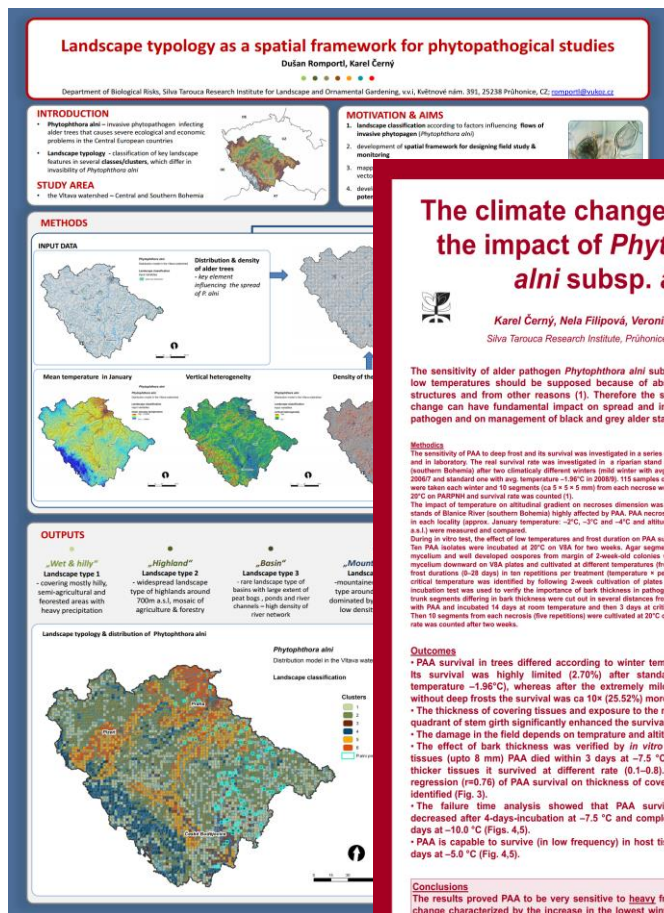
Rozšíření fytoftorového onemocnění olše a jeho přenos – cílová invazivní organismy *Phytophthora alni* v České republice
Černý K., Štrnadová V. & Filipová N., VÚMOP, v.v.i. Práhonice, 2010.



Phytophthora alni Brasier et S. A. Kirk

Plíseň olšová





The climate change can affect the impact of *Phytophthora alni* subsp. *alni*

Karel Černý, Nela Filipová, Veronika Strnadová
Silva Tarouca Research Institute, Píhoňovice, Czech Republic

The sensitivity of alder pathogen *Phytophthora alni* subsp. *alni* (PAA) to low temperatures should be supposed because of absence of resting structures and from other reasons (1). Therefore the supposed climate change can have fundamental impact on spread and importance of the pathogen and on management of black and grey alder stands.

Methods
The sensitivity of PAA to deep frost and its survival was investigated in a series of investigations in field and in laboratory. The real survival rate was investigated in a riparian stand of Mlýnský Dvůr River (southern Bohemia) after two climatically different winters (cold winter with avg. temperature 2.54°C in 2006/7 and standard one with avg. temperature -1.56°C in 2008/9). 115 samples of fresh necroses (Fig. 1) were taken each winter and 10 segments (5 × 5 × 5 mm) from each necrosis were cultivated 14 days at 20°C on PARPNH and survival rate was counted (1).
The impact of temperature on altitudinal gradient on necrosis dimension was investigated in riparian stands of Blatná River (southern Bohemia) highly affected by PAA. PAA necroses of 20 affected sides in each locality (approx. January temperature -2°C, -3°C and -4°C and altitude 400, 600 and 800 m a.s.l.) were measured and compared.
During *in vitro* test, the effect of low temperatures and frost duration on PAA survival was investigated. Ten PAA isolates were inoculated at 20°C on VJA for two weeks. Agar segments (diam. 0.5 cm) with mycelium and well developed sporangia from margin of 2-week-old cultures were cut out, plated by mycelium downward on VJA plates and cultivated at different temperatures (from -0.1 to -10.0°C) and frost durations (0-28 days) in ten repetitions per treatment (temperature × period). Survival rate and critical temperature was identified by following 2-week cultivation of plates at 20°C (2). Additional inoculation test was used to verify the importance of bark thickness to pathogen survival. Black alder trunk segments differing in bark thickness were cut in several distances from collar to top, infected with PAA and incubated 14 days at room temperature and then 3 days at critical temperature -7.5°C. Then 10 segments from each necrosis (five repetitions) were cultivated at 20°C on PARPNH and survival rate was counted after two weeks.

Outcomes

- PAA survival in trees differed according to winter temperature course. Its survival was highly limited (2.70%) after standard winter (avg. temperature -1.56°C), whereas after the extremely mild winter (2.54°C) without deep frosts the survival was ca 10× (25.52%) more successful.
- The thickness of covering tissues and exposure to the most heated (SW) quadrant of stem girth significantly enhanced the survival.
- The damage in the field depends on temperature and altitude (Fig. 2).
- The effect of bark thickness was verified by *in vitro* test. Under thin tissues (upto 8 mm) PAA died within 3 days at -7.5 °C, whereas under thicker tissues it survived at different rate (0.1-0.8). The significant regression (r=0.76) of PAA survival on thickness of covering tissues was identified (Fig. 3).
- The failure time analysis showed that PAA survival significantly decreased after 4-days-incubation at -7.5 °C and completely died after 2 days at -10.0 °C (Figs. 4,5).
- PAA is capable to survive (in low frequency) in host tissues at least 28 days at -5.0 °C (Fig. 4,5).

Conclusions
The results proved PAA to be very sensitive to heavy frost. The climate change characterized by the increase in the lowest winter temperatures (as hypothesized by IPCC) poses a significant risk for alder population in Europe.

On the other hand, it was also found out, that PAA is unexpectedly cold-tolerant and it is apparently capable to survive in roots in non-frozen water and soil at zero for a long time.

Outcomes were published (1,2) and verified by modelling (3).

(1) Černý K., Strnadová V. (2012). J. Phy. Bot. 58: 329-336. (2) Černý K. et al. (2012). Forest Syst. 21: 327-342. (3) Aspinall et al. (2014). Glob. Change Biol. doi:10.1111/gcb.12801.



Factors affecting *Phytophthora alni* distribution in State Forests of the Czech Republic

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Phytophthora alni (PA) is the most important pathogen of European alders. Besides losses in forests where it can be introduced with planting material (1). It is very important to know its real distribution in forests, its importance and possible ways of introduction.



Methods
The distribution of PA in forest stands was investigated with cooperation with State Forests in 2013. The information on distribution of phytophthora root and collar rot of alder showing typical symptoms of bleeding center) was collected from more than 400 stands covering the whole area of the Czech Republic. Data were evaluated in Statistics 8.0 with use of GLM. The determination of primary sources of infection in landscape was carried out in highly forested area (covering ca 420 km²) on the border between Central and Southern Bohemia during field investigation in 2009 - 2011. The presence of Phytophthora and Pythium pathogens was investigated in 13 forest nurseries covering the whole area of the Czech Republic in 2014. Ten plants from each nursery were repeatedly flooded and maintained at 20 °C. Segments of tissues of plants showing necroses were inoculated as described in (1). Acquired isolates were determined by standard methods (1,2).

Outcomes

- Phytophthora alder disease was identified in 53% stands.
- Presence of the disease was positively affected by presence of watercourse in the stand and volume of alder biomass (standing timber stock). Presence of the disease was negatively affected by altitude (p < 0.01).
- Watercourses were identified in 78% of diseased stands. Significant differences in damage according to width of the watercourse was identified (Fig. 1) and positive regression of disease impact to watercourse width was identified (p < 0.05).
- Median of age of affected stands was 38 years (the difference in age of affected and healthy stands was not found, Fig. 2).
- There were 34 hot spots of infection identified in the investigated area: 32 fishfarming ponds and 2 forest stands (Fig. 3).
- Presence of PA in forest nurseries was very low (Tab. 1).

Conclusions and speculation
Natural spread of the pathogen with water predominates over the spread via infected planting material in the area because of:
1) strong relation of pathogen presence in forests to watercourses,
2) high age and biomass volume of infected stands,
3) fishfarming ponds as dominating hot spots in landscape and
4) low frequency of PA in nurseries.

Similar pattern of pathogen distribution in landscape and its impact prevailing in riparian stands could be also awaited in other European countries and areas with less intensive alder management.

(1) Jung T., Blaschke M. (2004). Plant Pathol. 53: 197-200.
(2) Štěpánková P. et al. (2013). Plant Pathol. Sci. 49: 53-516.

Economical losses caused by *Phytophthora alni* in riparian stands. Typological study of Vltava River basin (Czech Republic)

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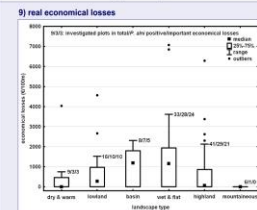
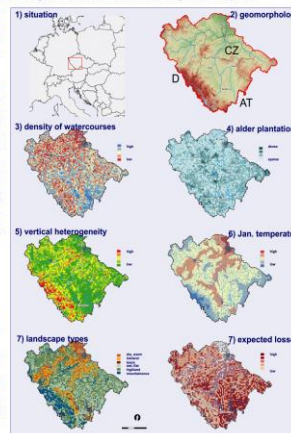
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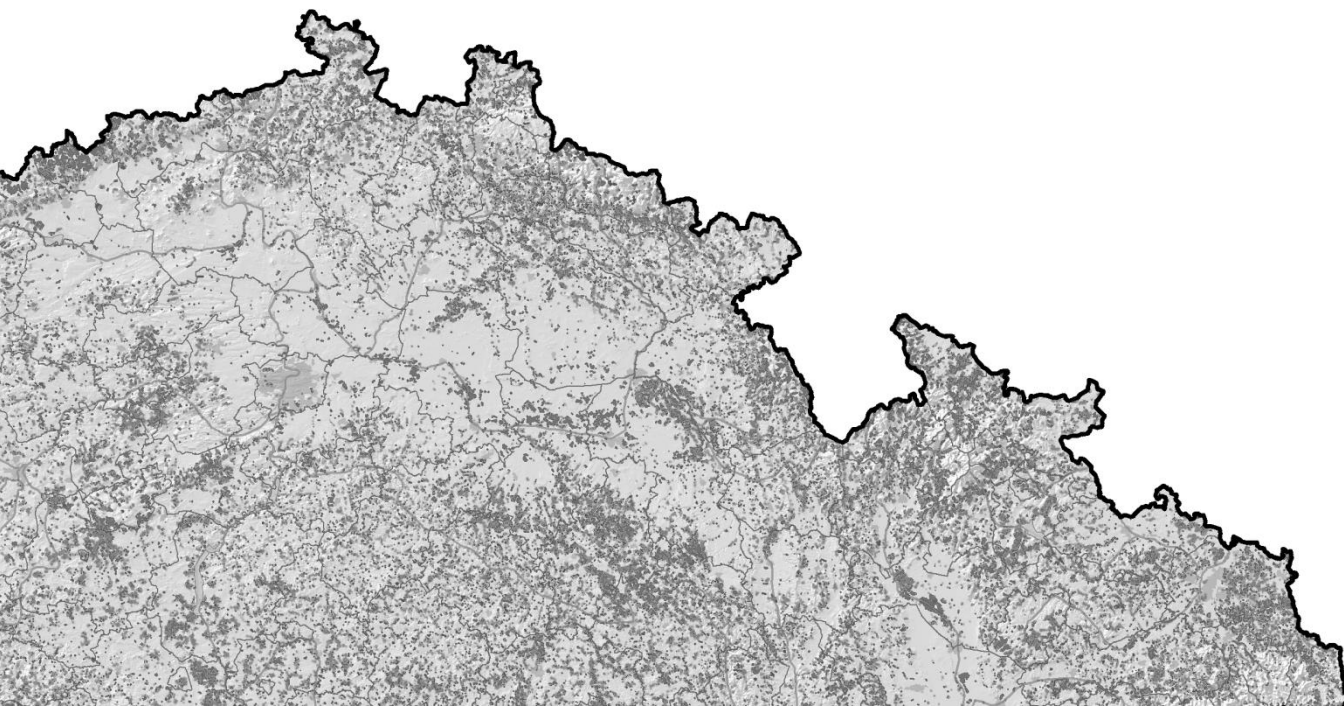
In recent years *Phytophthora alni* (PA) causes heavy and heterogeneously distributed losses in European riparian alder stands. It is necessary for river authorities to have basic information on economical losses caused by PA in different landscape types.

Methods. The Vltava River basin (VRB, Fig. 1,2) is highly affected by PA and serves as a model area. The information on pathogen distribution and ecology was summarized and the most important independent environmental factors influencing the pathogen distribution (density of river system, density of forest alder plantations, vertical heterogeneity and avg. January temperature; Figs. 3-6) were selected and used in a statistical model. VRB area was divided by rectangular grid (2.5 × 2.5 km), average values of variables were computed for all quadrates using GIS and quadrates clustered into 8 groups according to their environmental similarity (Fig. 7). The average values of all four variables were computed for each cluster and rank transformed. The ranks were averaged and ranking of clusters hypothetically corresponding to the PA impact was assembled (Fig. 8). Detection of PA distribution and evaluation of losses started in randomly selected quadrates in 2013. The economical losses in alder stands were computed according to applicable regulations evaluating the price of trees (1) and the cost of necessary works in affected alder stands - removing of dead and highly damaged trees and planting of substitutes (2).

Preliminary outcomes (2013, 116 quadrates)

- 71% of quadrates with PA.
- Important economical losses (EL) in 58% of quadrates.
- Average EL exceeded 1700 €/100 m of affected stand.
- Landscape types differed in EL (ANOVA, p < 0.05; Fig. 9)
- The most affected were wet and flat landscapes in middle altitudes and South Bohemian (pond) basins (Figs. 9,10).
- Less affected were valleys of broad rivers in lowlands and varied highlands with sparse water systems.
- Mountain landscapes with high vertical heterogeneity (and cold climate) and vice versa dry ad warm landscapes with low frequency of alder plantations were the least affected ones.
- Field data confirm applicability of the model.





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