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Dopad klimatických změn na lesní ekosystémy v Karpatech: změny biotického disturbančního režimu a možnosti adaptace lesa

Disertační práce

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Abstrakt

Karpaty představují jeden z nejrozsáhlejších souvislých lesních ekosystému v Evropě. Karpatské lesy jsou dlouhodobě intenzivně obhospodařovány, zároveň se zde však nacházejí mnohé původní ekosystémy s vysokou ekologickou hodnotou. V posledních desetiletích došlo v tomto regionu k výraznému nárůstu frekvence a intenzity biotických a abiotických disturbancí, které společně s exploatačním systémem obhospodařování výrazně narušily regionální ekosystémy. Narůstající intenzita disturbancí průkazně souvisí i s recentními změnami klimatu, které způsobují jak fyziologické oslabení dřevin, tak ovlivňují zejména biotický disturbanční režim. Projekce vývoje klimatu a výstupy ekosystémových modelů naznačují další nárůst intenzity disturbancí zahrnující např. nárůst rizika požáru, sucha, nebo invazi nových druhů škůdců.

Předložená práce se zaměřujeme na rozšíření poznatků o možných vlivech změny klimatu na disturbanční režim lesů v Karpatech. Práce představuje soubor publikovaných článků, které průřezově řeší (i) získání, zpracování a kontrolu kvality dat o lese pro celé území Karpat, (ii) vyhodnocení charakteru očekávané změny klimatu v Karpatech, (iii) analýzu vybraných aspektů biotického a abiotického disturbančního režimu Karpat a (iv) návrh doporučení pro management lesa podporující adaptaci na změnu klimatu s ohledem na disturbance. Řešení se opíralo o zpracování rozsáhlých souborů lesnických, environmentálních a dalších dat pomocí nástrojů GIS a sérii statistických analýz.

Studie Trombik a Hlásny (2013) se zaměřila na vyhodnocení kvality volně dostupných geodat o rozšíření lesa a dřevinné skladbě v Evropě. Byla zjištěna relativně vysoká přesnost dat opisujících rozšíření lesa, avšak korespondence dřevinné skladby s referenčními daty byla mimořádně nízká. V navazujících studiích byla ze všech karpatských států získána dlouhodobá data o dynamice hlavních škůdců a územích s různým stupněm ochrany přírody. Studie Hlásny, Trombik et al. (2016a) se zabývá vyhodnocením budoucí klimatické exponovanosti Karpat s využitím metodiky tzv. hot-spotů. Jedná se o lokality, ve kterých současně kulminuje změna většího počtu klimatických prvků oproti referenčnímu období. V celém území Karpat bylo identifikováno 8 hot-spotů klimatické změny, ze kterých většina byla lokalizována v nižších polohách. Tato skutečnost naznačuje stoupající riziko zejména pro již v současnosti vodou limitované ekosystémy. Studie Hlásny, Trombik et al. (2016b) se zaměřila na vyhodnocení dlouhodobé časové fluktuace bekyně mnišky (*Lymantria dispar*) v rámci Karpat a na vytvoření statistického modelu umožňujícího předpovídat další gradace. Poprvé byl identifikován vztah mezi narůstající zeměpisnou šířkou a délkou gradační periody jako i obecně odlišný charakter výskytu gradací mezi Západními Karpaty a jihovýchodní části Karpat. Čtvrtá studie (Holuša, Lukášová a Trombik 2013) se věnuje popisu prvních nálezů lýkožrouta severského (*Ips duplicatus*) uvnitř horských komplexů ve střední Evropě. Jedná se o druh pronikající z východu a potenciálně představující významné riziko i pro karpatské lesy. Tři studie (Trombik et al. 2016, Hlásny et al. 2017a) se zaměřují na modelování vývoje smrkových porostů v podmínkách napadnutí stromů lýkožroutem. Tyto práce poukázaly na rizika pěstování smrkových monokultur ve střední Evropě a předložily doporučení po jejich management zahrnující jak změnu dřevinné skladby, tak i úpravu doby obmýtí. V závěrečné studii Hlásny et al. (2014) jsou komplexně zpracována doporučení pro management lesa v podmínkách změny klimatu s důrazem na vývoj opatření ochrany lesa a monitoring škůdců. Tento soubor vědeckých studií je doplněn o 3 soubory certifikovaných map, které popisují vybrané aspekty současného a budoucího rozšíření hlavních škůdců v Karpatech.

Klíčová slova: lesní škůdci, populační dynamika, klimatická změna, ochrana lesa, adaptace

Abstract

Carpathians are one of largest continuous forest ecosystems in Europe. Carpathian forests have been intensively managed for a long time. At the same time however, Carpathians include numerous original and highly valuable ecosystems of European importance. In recent decades the region has been experiencing substantial increase in the frequency and intensity of biotic and abiotic disturbances, which, along with often exploitational use of resources, significantly disturbed the regional ecosystems. Body of evidence suggests that intensifying disturbances are related to climate change, which compromise plant vigour and affect biotic agents disturbing the forests. Climatic projections and simulations generated by ecosystem models indicate further intensification of forest disturbances, including increased risk of forest fires, drought or invasions of new pests and diseases.

This thesis strives to extend the current knowledge of climate change impacts on Carpathians and regional disturbance regimes. The thesis consists of the set of published papers, which systematically present (i) collection, pre-processing and quality control of the underlying forest data for the whole Carpathians, (ii) assessment of the patterns of climate change in the Carpathians, (iii) analyses of different aspects of biotic and abiotic disturbance regime of the Carpathians, (iv) proposal of recommendations for forest management, which can support climate change adaptation mainly with respect to forest disturbances. To reach these objectives, we analysed extensive forestry, environmental and other data using the tools of GIS and statistics.

The paper Trombik and Hlásny (2013) evaluated the quality of freely available data on forest distribution and species composition in Europe. We found good quality of data on forest distribution, but match of species composition maps with reference data was remarkably poor. In several follow-up studies we collected data on the dynamics of main forest pests and nature conservation areas from all Carpathian countries. The paper Hlásny, Trombik et al. (2016a) investigated the patterns of future climatic exposure of the Carpathians using the so-called hot-spot approach. The hot-spots are referred to as areas, where the projected change in several climatic variable culminates simultaneously. We identified eight climate change hot-spots in the Carpathians, most of them being distributed in lower-elevation areas. This indicates increasing risk for ecosystems in water-limited environments. Study Hlásny, Trombik et al. (2016b) investigated the long-term fluctuation patterns of Gypsy moth (*Lymantria dispar*) in the Carpathians and developed statistical forecasting model to predict the future outbreaks. The study identified, for the first time, the relationship between the geographical latitude and outbreak period length as well as differential outbreak patterns in the Western Carpathians and the south-eastern part of the region. This third study (Holuša, Lukášová and Trombik 2013) informs on the first findings of Northern bark beetle (*Ips duplicatus*) in the intra-mountain forests of central Europe. The beetle is an invasive pest penetrating from the east and representing potential risk also for the Carpathians forests. Other three studies (Trombik et al. 2016, Hlásny et al. 2017a,b) addressed the modelling of spruce forest development under bark beetle outbreak. The studies underscored risks related to the management of spruce monocultures in central Europe and formulated recommendations on their management, which included, for example, change of tree species composition of modification of rotation period. The final study Hlásny et al. (2014) provides systematic recommendations on forest management under climate change, with stress laid on improved forest protection and pest monitoring systems. The earlier mentioned research papers are complemented by three sets of certified maps, which present various aspects of present and future distribution of forest pests in the Carpathians.

Key words: forest pests, population dynamics, climate change, forest protection, adaptation

Obsah

1. Úvod

Karpaty jsou největší Evropský horský masiv, který prochází Rakouskem, Českou republikou, Slovenskem, Maďarskem, Polskem, Ukrajinou, Rumunskem a Srbskem (Ruffini et al. 2006). Vrcholy Karpat představují nejrozsáhlejší evropské oblasti horských lesů (ve výškách 950 až 1 350 m n.m.), nalezneme zde rovněž největší plochy přirozených bukových a jedlobukových lesních ekosystémů a největší plochu pralesních společenstev v Evropě (Werners et al. 2014). V Karpatech lze nalézt nejméně jednu třetinu všech evropských druhů cévnatých rostlin – 3 988 druhů rostlin, z nichž 481 se vyskytuje pouze v této oblasti (Bálint et al. 2011, Otypková et al. 2011). Horská společenstva jsou rovněž domovem největších evropských populací medvěda hnědého, vlka, rysa, zubra a vzácných druhů ptáků včetně např. orla královského (Salvatori et al. 2002). Přilehlé obydlené oblasti jsou s horami funkčně propojeny a využívají množství ekosystémových služeb skýtaných lesy (Gurung et al. 2009). Kromě toho je širší karpatský region domovem zhruba 17 milionů obyvatel žijících v malých komunitách až po středně velká městská centra (Csagoly 2007, Ruffini et al. 2008). Většinou se jedná o obyvatele zemí s přechodnou ekonomikou, pro které je typické nadměrné využívání přírodních zdrojů a další praktiky neudržitelného managementu (Schulze 2002; Knorn et al. 2012).

Probíhající změna klimatu má vliv na množství ekosystémů, lesy Karpat nevyjímaje (Linder et al. 2010, Hlásny et al. 2011). Současná intenzita oteplování je přibližně 0,2°C za rok, přičemž pro Střední Evropu je v porovnání s obdobím 1961-1990 projektován do konce století nárůst teploty vzduchu o 3-4°C a pokles ročních úhrnů srážek o 10 % (Christensen et al. 2007). Již výsledky současných pozorování a výzkumů indikují výrazné změny v jednotlivých biologických a krajinných systémech Karpat (např. Gurung et al. 2009, Spinoni et al. 2015). Pro lesy Karpat je do budoucna sucho jedním z nejzávažnějších rizik (Linder et al. 2010). Může působit jako primární mortalitní činitel, což je jev, který byl v Evropě doposud dokumentován zejména ve Středozemí (Allen et al. 2010) i jako predispoziční faktor pro napadení různými druhy škůdců a patogenů (Rouault et al. 2006), což je úkaz typický pro Střední a Severní Evropu. Frekvence extrémních hydrologických jevů se během posledních desetiletí prudce zvyšuje a pravděpodobně odráží současné změny klimatu v regionu (Easterling et al. 2000, Gurung et al. 2009). Výrazné zvýšení intenzity a frekvence bylo zaznamenáno i u lesních disturbancí, jedná se o zvýšenou frekvenci lesních požárů, větrných polomů, nebo přemnožení hmyzích škůdců (Hlásny a Sitková 2010, Temperli et al. 2013)

Změny různých aspektů chování škůdců a patogenů patří k nejvýraznějším projevům dopadů změny klimatu na les (Wermelinger 2004, Jönsson et al. 2007, Hlásny et al. 2011). Změna klimatu přímo ovlivňuje rozšíření, populační dynamiku, virulenci, nebo změny hostitelských dřevin mnohých biotických činitelů, a tím nepřímo ovlivňuje lesní ekosystémy (Netherer a Schopf 2010). Dosavadní poznatky naznačují, že v Karpatech bude stoupat riziko poškozování porostů kůrovci, zejména lýkožroutem smrkovým *(Ips typographus* Linnaeus 1758). Narůstat může i riziko poškozování porostů v současnosti méně významnými druhy, kterým je např. lýkožrout severský (*Ips duplicatus* Sahlber 1836). Z defoliátorů je možné za klíčového škůdce i do budoucna považovat bekyni velkohlavou (*Lymantria dispar* Linnaeus 1758), u které se předpokládá s klimatickou změnou související nárůst velikosti gradačních areálu (Logan et al. 2003; Hlásny a Turčáni 2009).

Výzkumu disturbančních režimů Karpat, managementu lesa, nebo vlivům změny klimatu se již věnovalo množství vědeckých studií (např. Bartholy et al. 2004, 2013, Kuemmerle et al. 2007, Svoboda et al. 2012, Temperli et al. 2013, Spinoni et al. 2015). Navzdory výsledkům těchto výzkumů zůstávají mnohé aspekty a zákonitosti možných dopadů klimatické změny na lesy Karpat nepoznány. Motivací pro řešení této práce je snaha doplnit a dále rozvinout současné poznatky o disturbančních režimech Karpat a možných vlivech změny klimatu a přispět tak k jejich udržitelnému managementu.

2. Cíle práce

Cílem této práce je zhodnotit specifické aspekty očekávaného vývoje klimatu v Karpatech, vyhodnotit a interpretovat změny v distribuci a populační dynamice hlavních škůdců. Předkládanou práci je možné rozdělit do následovných dílčích cílů:

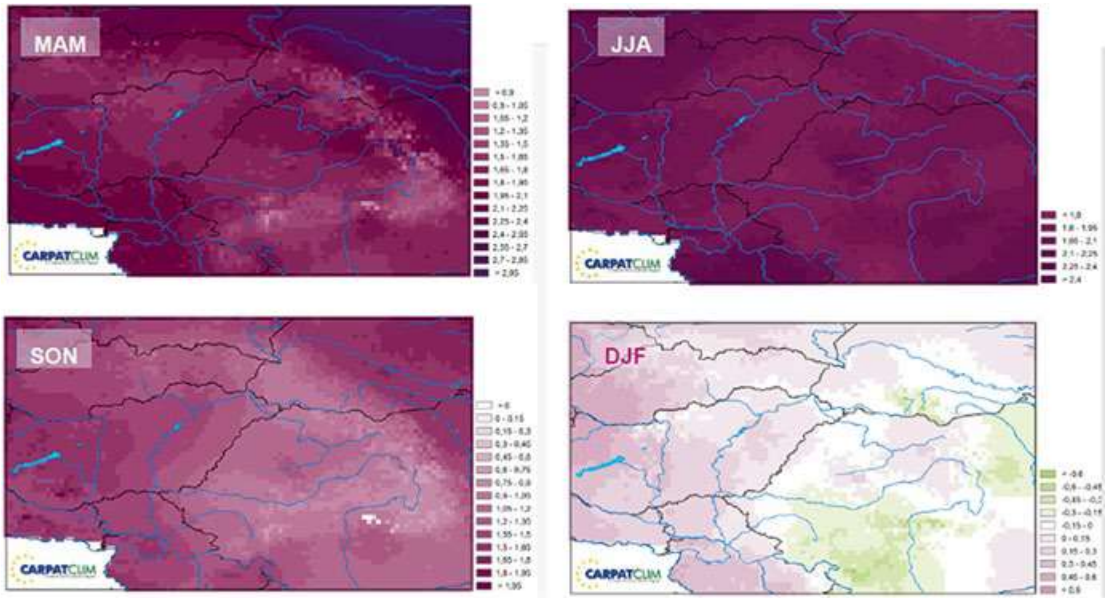
- Vytvořit geodatabázi obsahující celokarpatská data o abiotických složkách krajiny (půdy, geologie, klima), vegetaci (zejména informace o lese) a další podpůrná data jako hranice chráněných území, hustotu obyvatelstva apod.
- S využitím kolekce (ensemble) scénářů změny klimatu vyhodnotit očekávaný vývoj klimatu a klimatickou exponovanost jednotlivých regionů a výsledky interpretovat ve vztahu k lesním ekosystémům.
- Na základě rozboru literárních zdrojů a analýzy nashromážděných dat o výskytu a recentních změnách v aktivitě hlavních škůdců a patogenů v Karpatech ve vztahu ke změně klimatu formou samostatných studií vyhodnotit a interpretovat změny v časoprostorové dynamice a distribuci vybraných biotických škodlivých činitelů a zákonitosti jejich působení na lesy.
- Vyhodnotit celkovou zranitelnost lesních ekosystémů Karpat a vyvodit závěry pro management lesa, ochranu přírody a možnou adaptaci na změnu klimatu s důrazem na ochranu porostů vůči vlivu vybraných škodlivých činitelů.

3. Rozbor problematiky (literární rešerše)

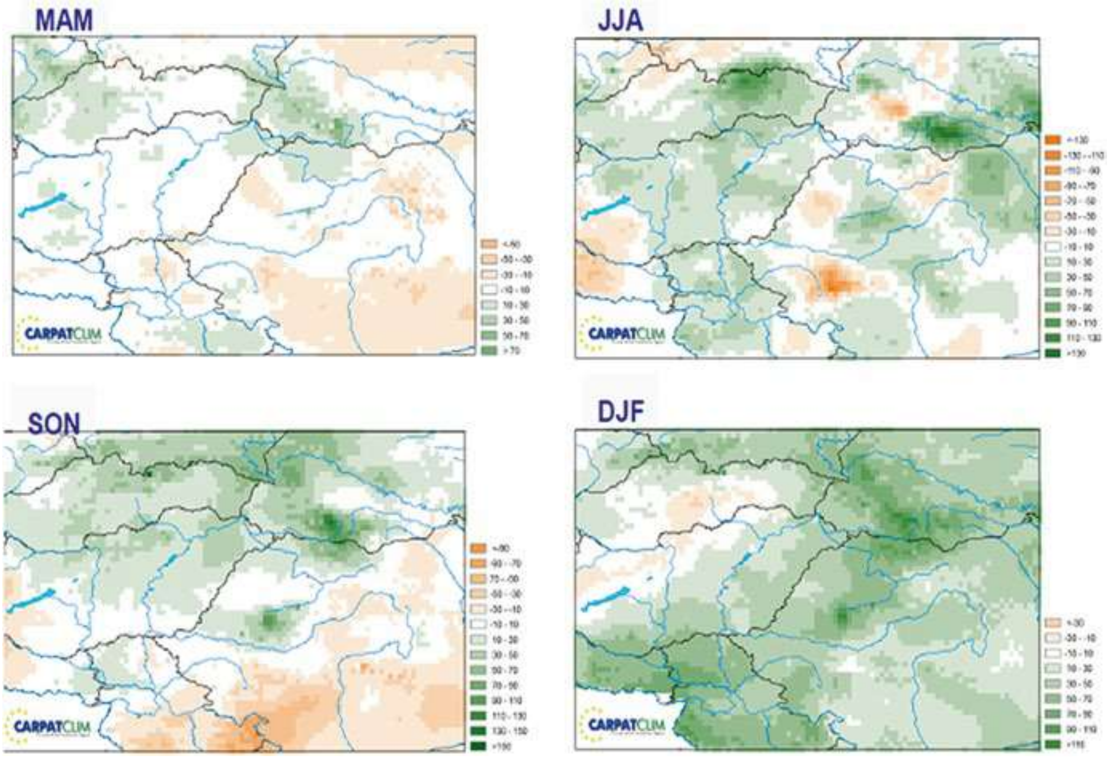
3.1 Současné trendy ve vývoji klimatu a klimatická změna v Karpatech

V posledních dvou desetiletích se na analýzu současných trendů ve vývoji klimatu a problematiku změny klimatu a jejich dopadů v regionu Karpat soustřeďují víceré evropské strategické materiály. Příkladem je projekt CARPIVIA (www.carpivia.eu) a Carpathian Convention (Weiss a Streifeneder 2011), jehož výsledkem je Atlas Karpatského makroregionu (Ruffini et al. 2008). V rámci projektu CARPATCLIM (Szalai a Vogt 2011) vznikl Atlas klimatu Karpatského regionu (Spinoni et al. 2015), který obsahuje homogenizovaná data pro 16 klimatických proměnných za období 1961-2010. Werners et al. 2014 a Spinoni et al. 2015 ve své práci analyzovali současné trendy ve vývoji klimatu v Karpatech, výsledky této studie lze shrnout v následujících bodech:

- Průměrné, maximální a minimální teploty vzduchu jsou závislé především na nadmořské výšce, nejteplejšími oblastmi v rámci regionu je jihovýchodní část Rumunska a Srbské Karpaty.
- Největší úhrny srážek lze pozorovat od května do června, nejvyšší roční srážkové úhrny se vyskytují v nejvyšších polohách (průměrně 1650 mm v Tatrách a Ukrajinských Karpatech). Nejnižší srážkové úhrny jsou na východě Maďarska (80 mm).
- Během období 1961-2010 došlo k výrazným změnám jak teploty vzduchy, tak i úhrnů a časového rozložení srážek (Obr. 3.1,3.2).
- Průměrná teplota vzduchu vzrostla na západě, východě a nižších polohách Karpat o 1,1 – 2,0 °C (Obr. 3.1), změny ve vyšších polohách byly méně průkazné. Většinou k oteplení docházelo v průběhu letních měsíců, v zimě průměrná teplota vzrostla pouze o 0,4 °C v rámci celého regionu (Obr. 3.1).
- V porovnání s teplotou jsou pozorované změny v úhrnu srážek mnohem více variabilní. Na západě a jihovýchodě území lze pozorovat úbytek srážek, zatímco na severu a severovýchodě srážky narůstají (Obr. 3.2).



Obr. 3.1 Nárůst průměrné teploty vzduchu v období 1961 – 2010 (jaro – vlevo nahoře; léto – vpravo nahoře; podzim – vlevo dole; zima – vpravo dole) podle Werners et al. 2014

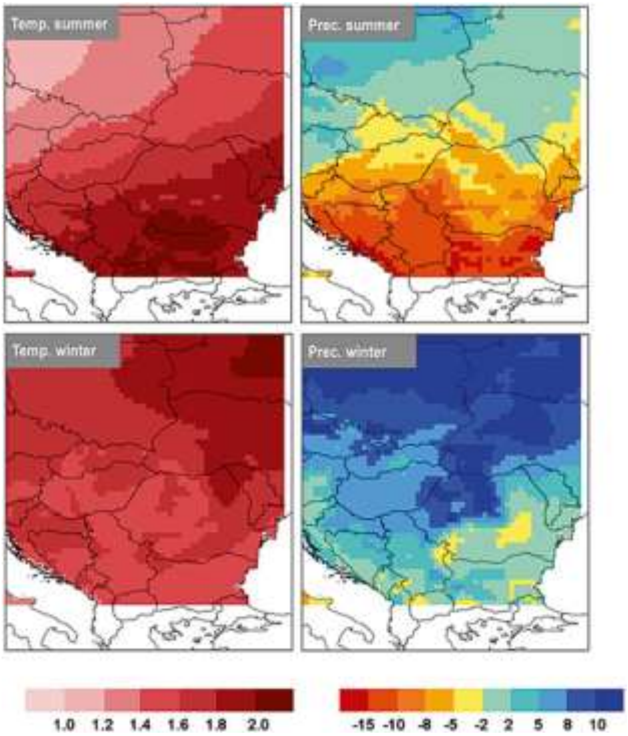


Obr. 3.2 Změna celkového úhrnu srážek v období 1961 – 2010 (jaro – vlevo nahoře; léto – vpravo nahoře; podzim – vlevo dole; zima – vpravo dole) podle Wernerse et al. 2014

Předpokládané změny klimatu byly v posledních letech také intenzivně studovány za pomocí historických měření a trendů (Bartholy et al. 2004, Bartholy a Pongrácz 2007) a pomocí regionální klimatických modelů jako PRECIS (Pieczka et al. 2010), RegCM3

(Busuioc et al. 1999, Torma et al. 2011) nebo COSMO-CLM (Anders a Haslinger 2013). Většina studií využívala informace v měřítku jednotlivých zemí karpatského regionu (např. Pongrácz et al. 2011, 2013, Bartholy et al. 2013, Micu et al. 2015) zahrnující pouze část území, nebo používala pouze omezený počet klimatických modelů (např. Belda et al. 2015). I přes tyto nedostatky se většina studií shoduje v hlavních bodech předpokládaných změn v klimatu Karpat:

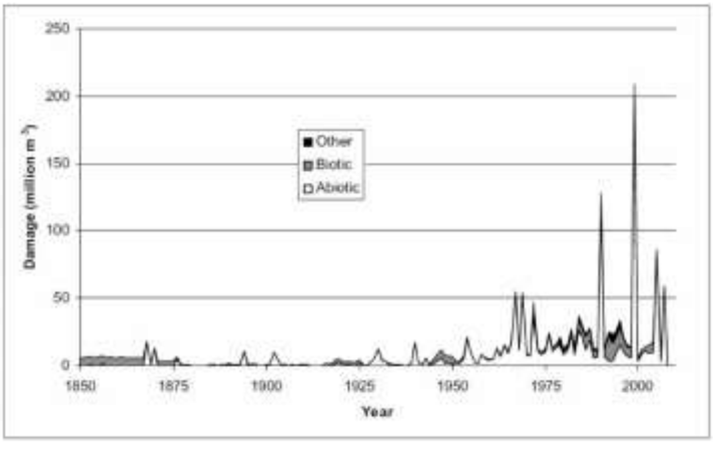
- Na konci tohoto století lze očekávat nárůst průměrné teploty vzduchu o 3,0 °C na severovýchodě a až 4,5 °C na jihu Karpatského regionu, oteplení bude výraznější v průběhu letních měsíců a méně pozorovatelné v zimě (Obr. 3.3).
- Ačkoli trend a shoda jednotlivých modelů není dokonale průkazná, lze očekávat úbytek srážek v letních měsících až o 20% a nárůst o 5-20% v průběhu zimy, zároveň lze předpokládat zkrácení doby se sněhovou pokrývkou (Obr. 3.3).
- Nárůst maximálních denních teplot a zvýšení počtu dnů s úhrnem srážek nad 20 mm.
- Předpokládané změny budou pravděpodobně mít značný dopad na výskyt a intenzitu period sucha. Nejvýrazněji se tato změna projeví ve vyšších polohách severozápadních a severovýchodních Karpat (Albert et al. 2013).



Obr. 3.3 Předpokládané změny v průměrné denní teplotě vzduchu (°C) (vlevo) a úhrnu srážek (%) (vpravo) mezi obdobími 2021-2050 a 1971-2000 (podle Alberta et al. 2013).

3.2 Disturbanční režim lesů a klimatická změna

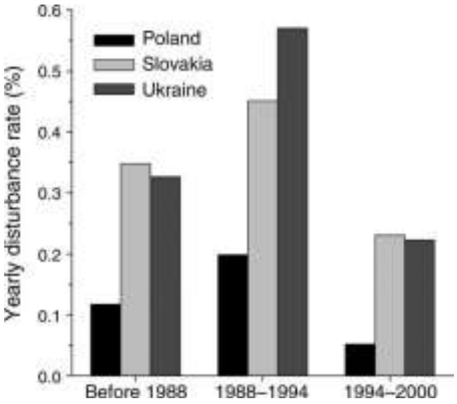
Disturbanční činitelé mají zásadní vliv na růst a celkovou produkci lesa, přičemž velkoplošné kalamity způsobují zhoršení poskytování celého komplexu ekosystémových funkcí (Schelhaas et al. 2003, Seidl et al. 2014). Především větrné polomy a lesní požáry hrají významnou roli v rámci hospodaření s obnovitelnými zdroji většiny zalesněných oblastí po celém světě (např. Baur et al. 2003, Prestemon a Holmes 2004). V období 1950-2000 bylo v Evropě komplexem disturbančních činitelů poškozeno ročně zhruba 35 mil. m^3 dřevní hmoty (Obr. 3.4), což odpovídá asi 8,1 % celkových těžeb v Evropě a asi 0,15 % z celkových zásob dřevní hmoty. Přibližně 53 % těchto škod je připisováno větrným polomům, 16 % lesním požárům a 3 % způsobil sníh. Biotičtí škodliví činitelé byli příčinou 16 % škod, z toho polovina škod je připisována kůrovcům. Přemnožení kůrovců jsou obvykle spojena právě s výskytem rozsáhlých větrných polomů (Nikolov et al. 2014). Vývoj poškození v pokalamitním období je zpravidla ovlivňován průběhem počasí v následujících letech (Schelhaas et al. 2003). Historický vývoj rozsahu i frekvence vzniku rozsáhlých disturbancí v Evropě ukazuje tendenci zvýšení poškození většinou škodlivých činitelů (Schelhaas et al. 2003, Seidl et al. 2014).



Obr. 3.4 Objemy nahodilých těžeb v rámci Evropy za období 1850-2000 (podle Schelhaase et al. 2003).

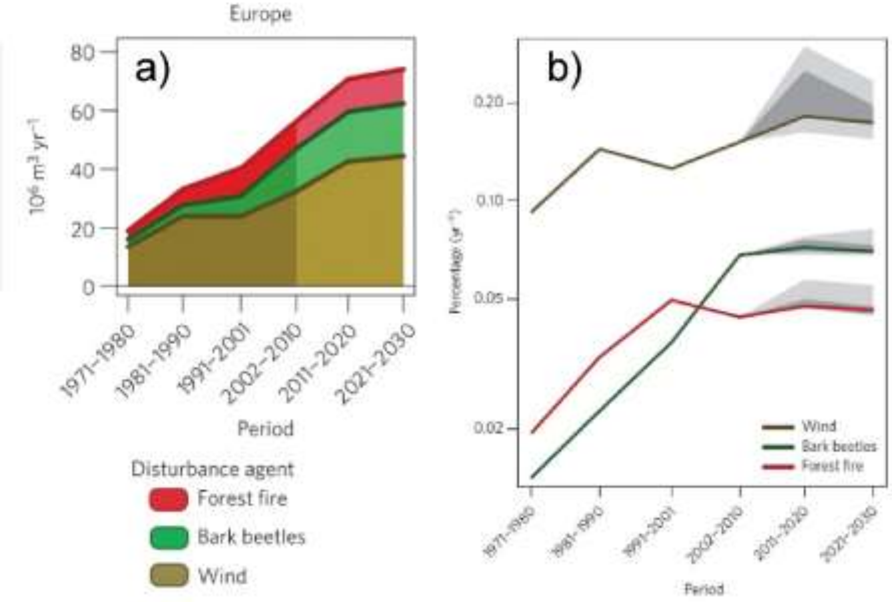
Podobnou situaci lze na základě regionálních studií pozorovat i v Karpatech (Kuemmerle et al. 2007, Temperli et al. 2013). V horské oblasti Karpat na pomezí hranic Slovenska, Polska a Ukrajiny bylo v letech 1978-2000 poškozeno celkově 510 km^2 lesa (téměř 3% všech lesů v oblasti), z toho 353 km^2 disturbancí vzniklo po roce 1988 (Obr.

3.5; Kuemmerle et al. 2007). Rozsah disturbancí vykazoval podobný trend ve všech 3 státech a od roku 1988 se zvýšil 1,3-1,8 krát (Obr. 3.5; Kuemmerle et al. 2007).



Obr. 3.5 Relativní rozsah disturbancí v pohraniční (slovensko-polsko-ukrajinské) části Karpat (podle Kuemmerleho et al. 2007)

Trend ve zvyšování počtu a narůstající intenzitě lesních disturbancí bude pod kombinovaným vlivem klimatické změny a antropogenního tlaku na lesy pravděpodobně narůstat i v dalších dekádách (Obr. 3.6; Seidl et al. 2011, 2014, Temperli et al. 2013). V mnoha oblastech po celém světě lze vývoj rozlohy, intenzity a frekvence disturbancí považovat za jeden z nejzásadnějších dopadů klimatických změn na lesní ekosystémy (Dale et al. 2001, Lindner et al. 2010, Turner 2010).



Obr. 3.6 Lesní disturbance v Evropě v letech 1971-2010 a jejich predikce na základě ensemblu klimatických modelů do roku 2030 v **a)** mil. m3 za rok **b)** roční procento disturbancí v poměru s celkovým přírůstem (šedé plochy představují mezi-modelovou variabilitu jednotlivých scénářů změny klimatu) (podle Seidla et al. 2014)

Přestože scénáře změny klimatu se vyznačují značnou variabilitou, je patrná obecná tendence k vyšším teplotám a větší proměnlivosti srážek (Meehl et al. 2007). I když je obtížné spolehlivě odhadnout frekvenci a intenzitu extrémních výkyvů počasí jakými jsou vichřice, epizody sucha či přívaly těžkého sněhu, je pravděpodobné, že se budou vyskytovat častěji než v minulosti (Kölling et al. 2010). Nedávné epizody sucha, jako Evropská vlna veder v roce 2003 (Rebetez et al. 2006), mají zásadní vliv na lesní ekosystémy (van Mantgem et al. 2009, Allen et al. 2010). S tímto faktem je také spojena větší četnost a závažnost lesních požárů (Westerling et al. 2006). Zvýšený stres vlivem sucha u hostitelských dřevin může rovněž oslabit jejich odolnost vůči napadení hmyzem (Malmstrom a Raffa 2000, Roy et al. 2004, Woods et al. 2005). Obecně jsou biotičtí škůdci mnohem citlivější a dokáží na změny klimatu rychleji reagovat (Bentz et al. 2010, Fisichelli et al. 2014), již v současnosti lze pozorovat změny v rychlosti vývoje jednotlivých škůdců (Logan et al. 2003), ploše a distribuci gradačních oblastí (Parmesan et al. 1999, Vanhanen et al. 2007, Hlásny a Turčani 2009, 2013), či zvýšené abundanci a významu nepůvodních či dříve nevýznamných škůdců a patogenů (např. Netherer a Schopf 2010, Duduman et al. 2011).

Dosavadní poznatky naznačují, že v Karpatech bude stoupat riziko poškozování porostů kůrovci, zejména lýkožroutem smrkovým (*Ips typographus*), narůstat může i riziko poškozování porostů v současnosti méně významnými druhy, jako je lýkožrout severský (*Ips duplicatus*). Význam těchto kůrovců je úzce svázán se zdravotním stavem porostů a vhodnými klimatickými podmínkami v daném místě. V současnosti se zpravidla líhnou dvě generace za rok, ve vyšších polohách jedna a při teplém průběhu počasí může být o jednu generaci více. Vyvíjí se téměř výhradně na smrku ztepilém (*Picea abies* (L.) H. Karst.), výjimečně na modřínu opadavém (*Larix decidua* Mill.) či jiných druzích jehličnatých dřevin. U lýkožrouta smrkového se předpokládá zkrácení doby vývoje, což mu umožní ukončit životní cyklus dříve a založit další generace během sezóny (Lange et al. 2006). Změna klimatu také ovlivní rojení, diapauzu a zimní mortalitu tohoto škůdce (Jönsson et al. 2007). Přestože je v porovnání s lýkožroutem smrkovým lýkožrout severský menším druhem (Pfeffer 1955) a pro vývoj by mu mohly stačit menší kumulativní teploty, v podmínkách střední Evropy *I. duplicatus* zpravidla kopíruje fenologický model *I. typographus* (Holuša et al. 2012). Hlavním rozdílem je fakt, že se *I. duplicatus* nevyskytuje ve vysokých nadmořských výškách (Holuša et al. 2010), ale preferuje polohy do 800 m n.m. (Holuša et al. 2013).

Z defoliátorů je možné za klíčového škůdce i do budoucna považovat bekyni velkohlavou (*Lymantria dispar*). Očekávané klimatické změny mohou rozšířit distribuční areál bekyně velkohlavé směrem na sever (Vanhanen et al. 2007) a také do vyšších nadmořských výšek (Hlásny a Turčáni 2009). V blízké budoucnosti se očekává značný nárůst plochy gradačních oblastí, nicméně další šíření tohoto škůdce může být limitováno výskytem dubových porostů jako primární hostitelské dřeviny. Teplejší a prodloužené léto může mít pozitivní dopad na růst a vývoj v nejsevernějších oblastech výskytu (Thomas et al. 1999, Vanhanen et al. 2007).

Zohlednění disturbančních procesů v rámci časoprostorového modelování dynamiky lesních a především smrkových porostů má zásadní význam (Franklin et al. 2002, Seidl et al. 2011). Smrkové porosty jsou historicky z velké části formovány velkoplošnými disturbancemi (Svoboda et al. 2012), které se v přírodě zpravidla vyskytují chaoticky a limitují jak lesnický management, tak i použití výsledků růstových a produkčních simulací (Weber a Flannigan 1997), které většinou pracují bez implementovaného disturbančního (mortalitního) scénáře (např. Seidl et al. 2008, Rötzer et al. 2009, Hlásny et al. 2011).

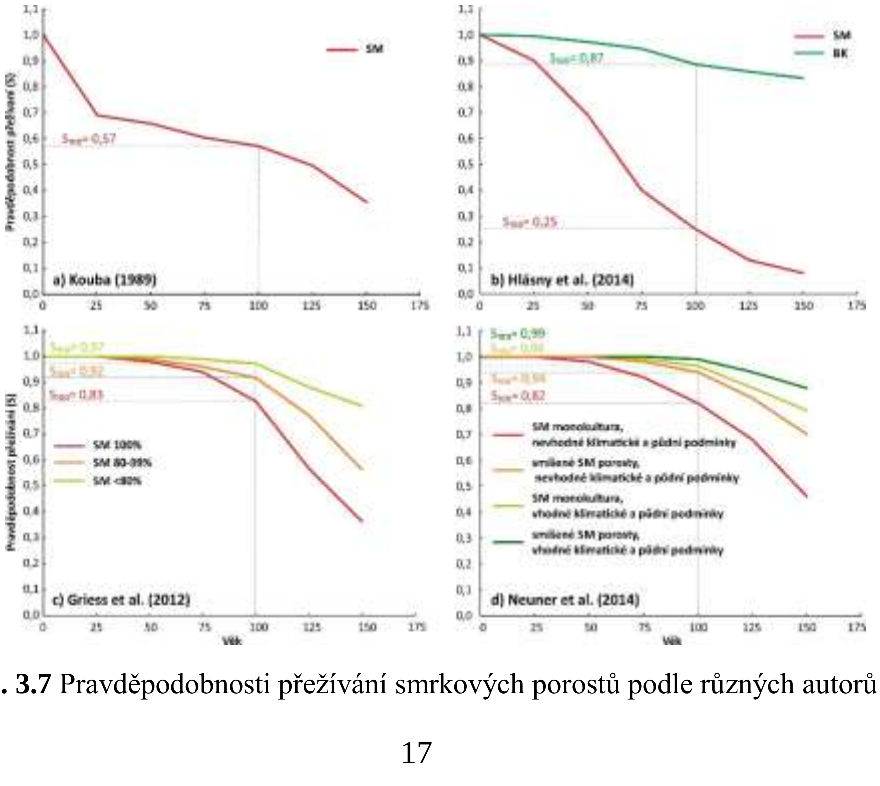
Předpovídání, dopady, očekávaný vývoj a interakce mezi jednotlivými disturbančními činiteli je v současnosti klíčovou problematikou ekologického a lesnického výzkumu (Buma 2015). Navzdory značnému pokroku v oblasti modelování přírodních škodlivých činitelů v lesních ekosystémech v posledních 20 letech (problematice se jen do roku 2010 věnovalo více než 300 vědeckých prací, které ve své práci zrevidoval Seidl et al. 2011) se většina postupů zaměřuje pouze na odhad zranitelnosti lesních komplexů jednotlivými činiteli, předpokládaný výskyt a intenzitu škod. Většina prací se rovněž zaměřuje pouze na jednotlivé disturbanční činitele a nezohledňuje vzájemnou interakci a synergický efekt celkového komplexu škodlivých činitelů (Turner 2010).

I nadále tedy zůstává implementace disturbančního režimu v modelování časoprostorové dynamiky lesa výzvou (Seidl et al. 2011). Obecně platí, že výskyt jednotlivých škůdců a škodlivých činitelů je závislý na interakci několika faktorů, např. klimatických a orografických podmínek, charakteristik porostu a prováděných lesopěstebních opatřeních (např. Gardiner a Quine 2000, Ruel 2000, Klopcic et al. 2009), proto analýza na úrovni jednotlivých faktorů neumožňuje hodnocení jejich integrálního vlivu.

Poměrně jednoduchý a praktický přístup, který může být použit v rámci růstových a jiných simulací, je určit hodnoty pravděpodobnosti výskytu nahodilých těžeb, resp.

simulovat mortalitu v jednotlivých věkových stupních vývoje porostu (Gadow 2000). Pravděpodobnosti přežívání jednotlivých stromů nebo porostů (tzv. survival probabilities) dle různých kritérií jsou nezbytným základem pro manažerské rozhodování v lesnictví, jako je například výběr dřevin či optimální doba obmýtí. Zařazení mortalitních pravděpodobností v modelech rovněž umožňuje zkoumat kombinovaný vliv disturbančních činitelů a očekávané budoucí změny klimatu. Pro tento účel již Kouba (1989) odvodil za použití empirických dat o poškození lesa a Weibullova rozdělení pravděpodobnost přežívání smrkových porostů, rizika spojená se zakládáním porostu a jejich poškozováním větrem a sněhem (Obr. 3.7).

Griess et al. (2012) použil na odvození funkcí přežívání dlouhodobé plochy monitoringu z jihozápadního Německa. Na základě série satelitních snímků od roku 1984 byl v této studii zkoumán vliv příměsi dřevin na pravděpodobnost přežití smrkových lesů. Výsledkem jsou na základě parametrů Weibullova rozdělení odvozené funkce přežívání v závislosti na zastoupení smrku v porostu (Obr. 3.7). Na tyto výsledky navázal ve své práci Neuner et al. (2015) v Bavorsku, kde byl do analýzy kromě zastoupení dřevin zahrnut rovněž vliv edafických a klimatických faktorů (Obr. 3.7). Studie Hlásny et al. (2014) uvádí příklad funkce pravděpodobnosti odvozené na základě dat lesní hospodářské evidence Slovenské republiky za období 1990-2010, která zahrnují údaje o nahodilých těžbách v důsledku všech relevantních disturbančních činitelů u všech hlavních dřevin (Obr. 3.7).



Obr. 3.7 Pravděpodobnosti přežívání smrkových porostů podle různých autorů.

Porovnání odvozených pravděpodobnosti přežívání podle jednotlivých autorů je zobrazeno v Tab. 3.1. Jak je možné vidět, jednotlivé pravděpodobnostní funkce se výrazně liší. Funkce odvozené na základě dat dlouhodobých pozorování s využitím dálkového průzkumu Země (Griess et al. 2012, Neuner et al. 2015) ukazují řádově vyšší procentuální pravděpodobnosti přežívání než v případě funkcí odvozených z empirických dat v České republice a na Slovensku (Kouba 1989, Hlásny et al. 2014; Kapitola 5.8). Výrazné rozdíly jsou dány jak užitou metodou, tak i rozdílnou historii hospodaření, dřevinným složením a regionálním disturbančním režimem. Velkou výhodu funkcí odvozených z dat LHE Slovenské republiky je možnost odvození mortalitních funkcí na základě stanoviště resp. jednotlivých tzv. klimatotopů (prostorové jednotky vzniklé překrytím vegetační stupňovitosti a hydrické řady podle metodiky publikované v práci Kulla a Bošeľa 2013). Naopak uvedené funkce nezohledňují pozitivní dopady příměsi jiných dřevin, které ovšem zohledňují práce Griess et al. (2012) a Neuner et al. (2015).

Tab. 3.1 Přehled pravděpodobnosti přežívání smrku podle věkových stupňů podle různých autorů.

Věk	**Kouba (1989)**	***Griess et al. (2012)**			****Neuner et al. (2015)**				**Hlásny et al. (2014)**
		100%	**80-99%**	**< 80%**	**m-v**	**s-v**	**m-n**	**s-n**	
0	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00
25	0,69	1,00	1,00	1,00	1,00	1,00	1,00	1,00	0,90
50	0,66	0,98	0,99	1,00	1,00	1,00	0,98	1,00	0,69
75	0,61	0,94	0,96	0,99	0,99	1,00	0,92	0,98	0,40
100	0,57	0,83	0,92	0,97	0,96	0,99	0,82	0,94	0,25
125	0,50	0,57	0,77	0,88	0,88	0,94	0,68	0,84	0,13
150	0,36	0,36	0,56	0,81	0,79	0,88	0,46	0,70	0,08

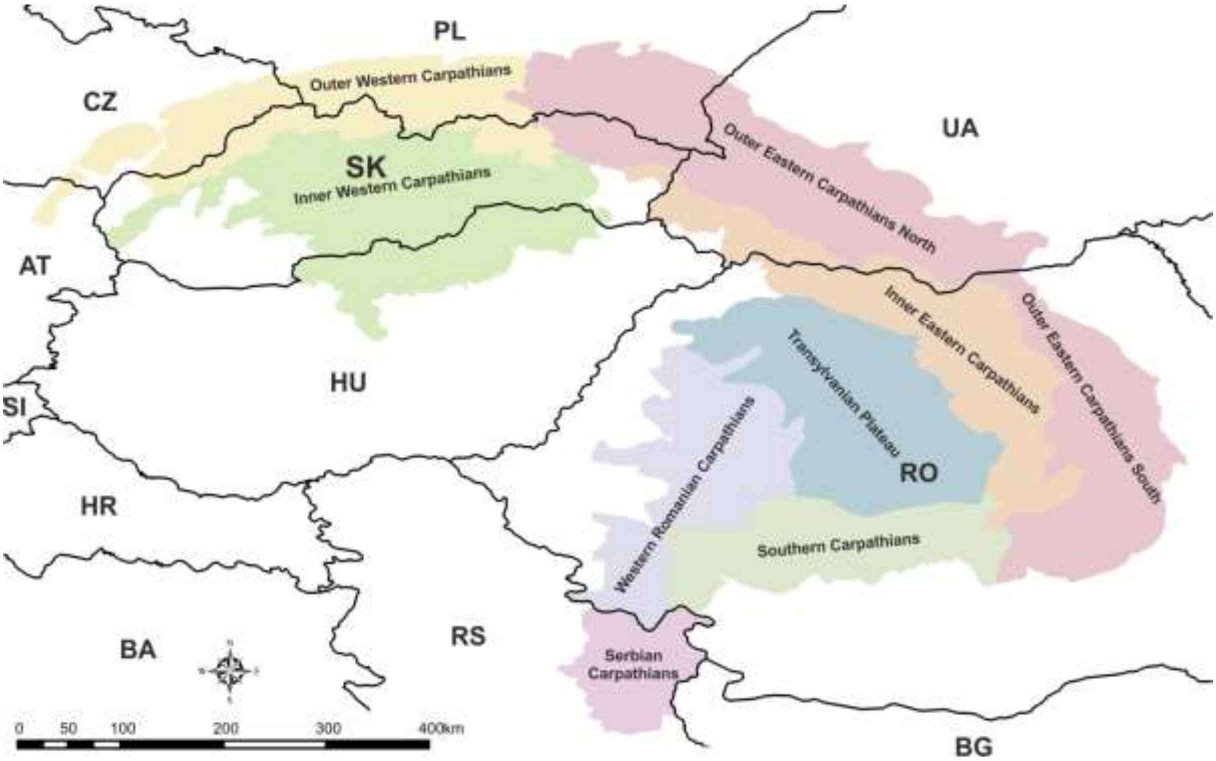
* zastoupení SM v porostu

** m – monokultura; s – smíšený porost; v – vhodné klimatické/půdní podmínky; n – nevhodné klimatické/půdní podmínky

4. Metodika

4.1 Vymezení území Karpat

V rámci předložené dizertační práce bylo území Karpat vymezeno kombinací hranic navržených Carpathian Ecoregion Initiative (CERI, http://www.carpates.org/) a Carpathians Environment Outlook (KEO 2007) (Obr. 4.1). Celková rozloha vylišeného regionu je 229 966 km^2 a pokrývá jak hlavní horské pásmo Karpat, tak i přilehlé vrchoviny a nížiny (celkové výškové rozpětí 27 – 2 604 m n.m.). Díky tomu se v rámci tohoto regionu vyskytuje široká škála lesních ekosystémů a typů využití krajiny. Lesy pokrývají 48% území, z toho 19% jehličnaté, 59% listnaté a 22% smíšené lesy (CORINE LandCover 2000, EEA 2006 a,b). Studované území bylo pro jednotlivé analýzy dále rozděleno na základě geomorfologických subprovincií podle Kondrackiho 1989 (Obr. 4.1), jejich stručná charakteristika je uvedena v Tab. 4.1.



Obr. 4.1 Vymezení území Karpat a použité geomorfologické rozdělení

Tab. 4.1 Charakteristika geomorfologických subprovincií v rámci území Karpat

Subprovincie	Plocha (km^2)	T (°C)	P (mm)	Procento plochy v rámci jednotlivých států
Jižní Karpaty	19,019	6.7	703	RO 100
Západní Rumunské Karpaty	22,968	6.8	639	RO 100
Srbské Karpaty	9,607	9.7	642	Serb 100
Transylvánská plošina	29,664	8.4	485	RO 100
Vnitřní východní Karpaty	27,971	6.9	704	RO 77, UA 21, SK 2
Vnější východní Karpaty - sever*	35,974	6.9	878	UA 60, PL 29, SK 11
Vnější východní Karpaty - jih*	23,545	7.9	558	RO 100
Vnitřní západní Karpaty	36,561	7.7	683	SK 68, HU 32
Vnější západní Karpaty	24,659	7.1	773	PL 38, CZ 30, SK 30, AU 3

Zkratky: CZ – Česká republika; SK – Slovensko; PL – Polsko; HU – Maďarsko; UA – Ukrajina; RO – Rumunsko; RS – Srbsko; T (°C) – průměrná roční teplota; P (mm) – průměrný roční úhrn srážek v období 1961-1990

* Vnější východní Karpaty byly dále rozděleny na dvě části („sever“ a „jih”) Ukrajinsko-Rumunskou hranicí z důvodu intenzivních rozdílů u klimatických prediktorů jednotlivých subregionů.

4.2 Struktura a obsah geodatabáze

Základem pro veškeré analýzy, tvorbu a interpretaci výsledku bylo vytvoření geodatabáze obsahující celokarpatská **data o klimatu** včetně scénářů očekávaného vývoje, vegetaci (zejména **informace o distribuci a dřevinném složení lesů**), **data o poškozování lesa** vybranými škodlivými činiteli a další **podpůrná data** jako hranice chráněných území, hustota obyvatelstva apod. Údaje o výškové zonálnosti byly převzaty z Shuttle Radar Topographic Mission (SRTM) **digitálního výškového modelu** (DEM), který je volně dostupný v rozlišení 90 a 250 m (Jarvis et al. 2008). Pro všechny státy v rámci regionu byla opatřena data o administrativním členění podle nomenklatury územních statistických jednotek (**administrativní jednotky** NUTS 0 - 3 a LAU 1 a 2), případně podle dostupnosti hranice lesních oblastí, biogeografických regionů apod.

Veškerá prostorová data byla transformována z národních souřadnicových systémů (např. Křovákovo S-JTSK pro Slovensko a ČR) do Lambertova azimutálního zobrazení

(Lambert Azimuthal Equal Area - LAEA) na elipsoidu ETRS pomocí nástrojů ArcInfo (ESRI 2010). ETRS LAEA byl systém všech hodnocených datových souborů. Tabulkové, obrazové, případně jiné analogické podklady byly do geodatabáze převedeny za použití nástrojů GIS (georeferencování, propojení jednotlivých datasetů pomocí jedinečných ID apod.). Obecný princip vzniku, struktury a obsah databáze je zobrazen na Obr. 4.2, jednotlivé datasety jsou podrobněji popsány v kapitolách 4.2.1-4.2.4.

Obr. 4.2 Schéma obsahu a struktury vytvořené celokarpatské databáze

4.2.1 Data o distribuci a dřevinném složení lesa a hodnocení jejich přesnosti

Byly shromážděny v současnosti veškeré volně dostupné celoevropské datasety o distribuci lesních ekosystémů. Základní parametry jednotlivých mapových setů jsou uvedeny v Tab. 4.2, jednotlivé datasety lze na základě obsažených informací rozdělit na dvě skupiny:

1) Vektorové a rastrové vrstvy nesoucí informaci o distribuci krajinného pokryvu „les“, v některých případech dále rozdělného na lesy jehličnaté, listnaté a smíšené. Jedná se hojně využívanou databázi CORINE Land Cover (2006 a,b) a čtyři celoevropské rastry (EFMAP 2002 - Schuck et al. 2002; FMAP 2000 - Pekkarinen et al. 2009; EFMAP 2011 - Gunia et al. 2011; FTYP 2006; FMAP 2006 -Kempeneers et al. 2011).
2) Vektorové a rastrové vrstvy nesoucí informaci jak o distribuci lesa, tak i jeho druhové skladbě. V rámci řešení jsme testovali 4 datové sety:
   a. Rozšíření dřevin EUFORGEN (EUFORGEN - EUFORGEN 2009).
   b. Druhová skladba lesů podle dat iniciativy Forest Focus (FMOD - FORESTMOD 2013).
   c. Druhová skladba lesů na základě statistického vyhodnocení zkusných ploch (TMAP 2009 - Tröltzsch et al. 2009; TMAP 2011 - Brus et al. 2011).

Kvalita jednotlivých mapových setů byla hodnocena na základě porovnání s aktuálními lesními hospodářskými plány (LHP) Slovenska. Hodnocení přesnosti bylo zaměřeno na porovnání rozsahu kategorií lesů v hodnocených datových souborech s údaji z LHP Slovenska v rámci FAD. Podrobněji je metodika popsána v publikaci Trombik a Hlásny 2013 (Kapitola 5.1 str. 37-40).

Tab. 4.2 Základní parametry jednotlivých datasetů o distribuci lesa

Dataset	Formát	Rozlišení	Pokrytí	Zdroje dat	Kategorie	Atributy	Udávaná přesnost
CORINE 2006	raster, vektor	1 : 100,000; 100x100m; 250x250m	EU-27, Abánie, Bosna a Hercegovina, Chorvatsko, Makedonie a Lichtenštejnsko	satelity Landsat a Spot, národní topografické mapy, letecké snímky, statistické údaje	lisnaté, jehličnaté a smíšené lesy	Presence/ absence	více než 85%
EFMAP 2002	raster	1x1 km	všechny evropské státy od Portugalska po Ural, vyjma Kypru a Turecka	AVHRR-NOAA; Národní inventarizace	les/neles; listnaté; jehličnaté	les ano/ne; procento zastoupení kategorie lesa	variabilní, průměrně ± 5%,
FMAP 2000	raster	25x25 m	EU-27, Norkso, Švýcarsko, Lichtenštejnsko, Albánie, Chorvatsko, Makedonie, Černá hora a Srbsko	Landsat ETM+ snímky; Corine LandCover 2000	les/neles	Presence/ absence	více než 80%
FMAP 2006 **FTYP 2006**	raster	25x25 m	EU-27, Norkso, Švýcarsko, Lichtenštejnsko, Albánie, Chorvatsko, Makedonie, Černá hora, Srbsko a Turecko	IRS-LISS-3; SPOT4/5; Corine LandCover 2000	les/neles; listnaté; jehličnaté	Presence/ absence	více než 80%
EFMAP 2011	raster	1x1 km	jako FMAP 2006 + Bělorusko, Ukrajina, Moldavsko a Rusko	satelity IRS-LISS-3; SPOT4/5; Corine LandCover 2000 a AVHRR-NOAA; Národní inventarizace	les/neles	Zastoupení lesa (%)	více než 80%; nižší pro Bělorusko, Ukrajinu, Moldavsko a Rusko
EUFORGEN	vektor	nespecifikováno	všechny evropské státy, vyjma Kypru, Turecka a Ruska	národní experti; dostupná literatura	34 dřevin	Presence/ absence	nespecifikována
TMAP 2009	raster	1x1 km	všechny evropské státy, vyjma Makedonie, Kypru, Ruska kromě Kaliningradského regionu, Andory a Lichtenštejnsko	plochy ICP Level 1; Národní inventarizace; vybrané proměnné prostředí	6 dřevin	Zastoupení dřeviny (%)	variabilní mezi jednotlivými státy, korelace s validačními daty mezi 0,2 – 0,8
TMAP 2011	raster	1x1 km	všechny evropské státy, vyjma Makedonie, Kypru, Ruska kromě Kaliningradského regionu, Andory a Lichtenštejnsko	NFI výzkumné plochy; Národní inventarizace; vybrané proměnné prostředí	20 dřevin	Zastoupení dřeviny (%)	43%, velká variabilita mezi jednotlivými dřevinami
FORESTMOD	raster	1x1 km	EU-27, Norkso, Švýcarsko, Lichtenštejnsko, Albánie, Chorvatsko, Makedonie, Černá hora a Srbsko	FMAP 2000; Forest Focus databáze	24 dřevin	Zastoupení dřeviny (%)	nespecifikováno, velká variabilita mezi jednotlivými dřevinami

4.2.2 Podpůrná data – využití krajiny, hranice chráněných území a hustota obyvatelstva

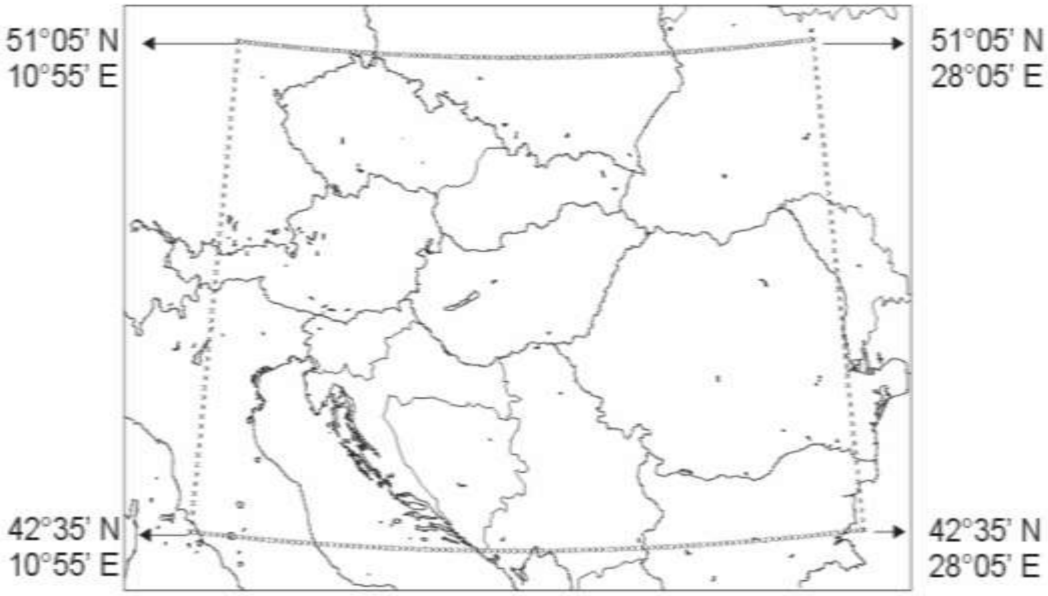
Kategorie využití krajiny (tzv. Land cover popř. Land use) byly převzaty z databáze Corine Land Cover (EEA 2006, CLC), jelikož tato databáze neobsahuje území Ukrajiny, byl dataset doplněn o vyhodnocené satelitní snímky Landsat, z nichž byl typ využití krajiny odvozen se souladem s CLC (Hlásny et al. 2016a; Kapitola 5.2 str. 64-65). Klasifikace byla založena na Maximum Likelyhood Classifier. Spektrální chování klasifikovaných kategorií Land cover bylo odvozeno ze spektrálních údajů o odrazivosti z obrazů Landsat v kategoriích CLC v regionech sousedících s Ukrajinou (na Slovensku, v Polsku a v Rumunsku). **Přírodní vegetace** Karpat byla odvozena na základě a map vytvořených Bohnem et al. (2004). Informace o nelesní vegetaci byly převzaty z několika zdrojů, např. Carpathian Biodiversity Information System (CBIS, Carpathian EcoRegion Initiative), nebo Carpathian Integrated Biodiversity System (CCIBIS, WWF Danube-Carpathian Programme).

Mapa **velkoplošných chráněných území** v Karpatech byla odvozena kombinací vnitrostátních databází, volně dostupné mapy karpatské sítě zvláště chráněných území (http://www.carpathianparks.org) a lokalit NATURA 2000. **Hustota obyvatelstva** byla odvozena na základě gridu populační hustoty pro EU (Gallego 2010). Protože tento soubor map nezahrnuje Srbsko a Ukrajinu, pro tyto státy byla použita méně přesná data založená na místních správních jednotkách (LAU 1) (Ruffini et al. 2006).

4.2.3 Klimatická data a metodika hodnocení klimatické exponovanosti Karpat

Použitá klimatická data byla převzata z databáze FORESEE (Dobor et al. 2015). Tato datová sada je založena na výsledcích měření meteorologických stanic (referenční období) a výsledcích klimatických modelů (budoucí období). Parciální výsledky byly použity k vytvoření denní meteorologické databáze pro celou oblast střední Evropy (Obr. 4.3) v letech 1951-2100, která obsahuje minimální / maximální teplotní a srážkové časové řady. Referenční období (1951-2009) je založeno na základě denní databáze E-OBS (vytvořená v rámci projektu FP6 ENSEMBLES, Haylock et al. 2008) a měsíční CRU TS 1.2 (Climatic Research Unit, University of East Anglia). Pro popis budoucího klimatu bylo vybráno deset RCM-GCM (Regionální klimatický model - globální klimatický model, Tab. 4.3) (údaje jsou poskytnuty v rámci projektu ENSEMBLES FP6, van der Linden et al. 2009), u nichž byla provedena korekce zkreslení pro období 1951-2100.

Všechny použité RCM byly řízeny scénářem emisí skleníkových plynů A1B (vyvážený důraz na všechny zdroje energie, IPCC 2000). Data byla interpolována na společnou vodorovnou rozlišovací sílu 1/6 × 1/6 stupně pomocí techniky interpolace inverzní vzdálenosti.



Obr. 4.3 Pokrytí databáze FORESEE (tečkovaný čtverec) obsahující klimatická data za období 1951-2100. Data jsou uloženy v 5,408 (104×52) pixelových buňkách v rámci pravidelné sítě 1/6×1/6°.

Tab. 4.3 Použité RCM v rámci FORESEE databáze.

ID	Název modelu (RCM-GCM)	Autor
1	ALADIN-ARPEGE	National Centre for Meteorological Research (CNRM)
2	CLM-HadCM3Q0	Swiss Federal Institute of Technology Zürich (ETHZ)
3	HadRM3Q0-HadCM3Q0	Hadley Centre for Climate Prediction and Research (HC)
4	HIRHAM5-ARPEGE	Danish Meteorological Institute (DMI)
5	HIRHAM5-ECHAM5	Danish Meteorological Institute (DMI)
6	RACMO-ECHAM5	Royal Netherlands Meteorological Institute (KNMI)
7	RCA-ECHAM5	Sweden's Meteorological and Hydrological Institute (SMHI)
8	RCA-HadCM3Q0	Sweden's Meteorological and Hydrological Institute (SMHI)
9	REGCM-ECHAM5	The Abdus Salam International Centre for Theoretical Physics (ICTP)
10	REMO-ECHAM5	Max-Planck-Institute for Meteorology (MPI)

K vytvoření celokarpatských rasterů ve vysokém rozlišení byla použita geostatistická metoda interpolace s externím driftem. Jako podpůrná proměnná při interpolaci byla použita data DMT v rozlišení 250 m. Podrobný popis této metody interpolace klimatických dat je uveden v práci Vizi et al. (2011).

Byla hodnocena tři období – 1961-1990 (referenční klima, založena na E-OBS datech) a období 2021-2050 a 2071-2100 (blízká a vzdálená budoucnost, založena na RCM v Tab. 4.3).

Na základě takto sestavených scénářů změny klimatu byl hodnocen vývoj výskytu a intenzity sucha v širším regionu střední Evropy (oblast západních Karpat). S ohledem na objevené trendy a očekávaný vývoj byly rovněž hodnoceny možnosti adaptace lesních porostů pomocí úpravy dřevinného složení (směrem k vyššímu zastoupení sucho tolerujících dřevin) a význam umělé obnovy jako možného adaptačního opatření. Podrobněji je problematika popsána v publikaci Hlásny et al. 2014 (Kapitola 5.8).

Při hodnocení klimatické exponovanosti Karpat v důsledku klimatických změn byla použita modifikovaná metoda navržená Diffenbaughem a Giorgimem (2012), která využívá standardní Euklidovou vzdálenost (SED) pro kvantifikaci agregované klimatické změny (ACC) v multidimenzionálním klimatickém prostoru mezi současným a budoucím obdobím (Williams et al. 2007). Při identifikaci hotspotů byly použity tyto klimatické proměnné:

- celkový úhrn srážek během vegetační sezóny (duben - září) (PTGS)
- počet po sobě jdoucích dní bez srážek (CDD)
- počet tropických dní (maximální teplota vzduchu během dne přesáhne 30°C) (T30)
- Ellenbergův klimatický koeficient (EQ)
- délka vegetační sezóny (GSL)

Hodnoty ACC byly vypočítány pro všech deset RCM, jejich průměrná hodnota byla použita pro identifikaci jednotlivých hotspotů. Podrobněji je metodika identifikace hotspotů a výběru proměnných popsána v publikaci Hlásny et al. 2016a (Kapitola 5.2 str. 48-50).

4.2.4 Data o poškozování lesa vybranými lesními škůdci a patogeny

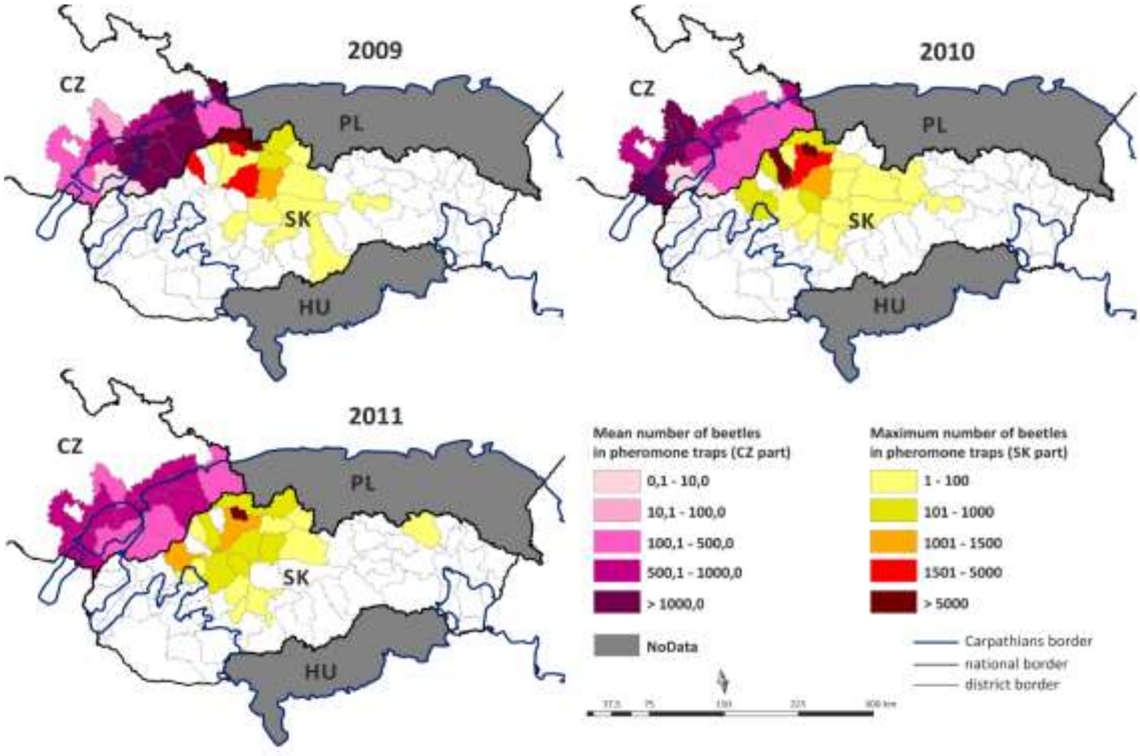
Pro sestavení databáze, výskytu a rozsahu jednotlivých škodlivých činitelů bylo využito výročních zpráv a databází národních ústavů a organizací ochrany lesa, vědeckých prací zabývající se jednotlivými škůdci, případně jiných interních materiálů. Byly získány informace o následujících škůdcích (z důvodu značného rozsahu databáze jsou výsledné hodnoty a mapové výstupy v této práci předloženy na příkladu *I. duplicatus* v kapitole 4.2.4.1) :

- **Defoliátoři:** *Cephalcia abietis; Cephalcia alpine; Cephalcia arvensis*; *Lymantria dispar*; *Lymantria monacha*; *Operophtera brumata*; *Pristiphora abietina*; *Thaumetopoea processionea*; *Tortrix viridana*.
- **Podkorní hmyz:** *Agrilus biguttatus, Agrilus viridis*; *Hylobius abietis*; *Ips amitinus*; *Ips duplicatus*; *Ips typographus; Polygraphus poligraphus; Taphrorychus bicolor*; *Tetropium castaneum*; *Tetropium gabrieli*; *Dreyfusia nordmannianae*.
- **Houbové patogeny:** *Phytophthora* sp.; *Armillaria* sp; *Sirococcus conigenus*; *Chalara fraxinea*.

Úroveň uvedených podrobností i prostorového rozlišení se mezi jednotlivými druhy značně liší, jelikož znalosti o ekologii škůdců, distribuci a vlivu změny klimatu jsou proměnlivé a obecně jsou systematicky sledovány a studovány pouze druhy s klíčovým významem pro lesnictví. Z tohoto důvodu nejsou získaná data pro jednotlivé druhy jednotná a následné analýzy a prediktivní modely vývoje byly vytvořeny pouze pro druhy, pro které byly shromážděny dostatečné informace a zároveň byly evaluací získaných dat zjištěny nové poznatky. Jedná se o lýkožrouta smrkového *Ips typographus*, lýkožrouta severského *Ips duplicatus* a bekyni velkohlavou *Lymantria dispar*.

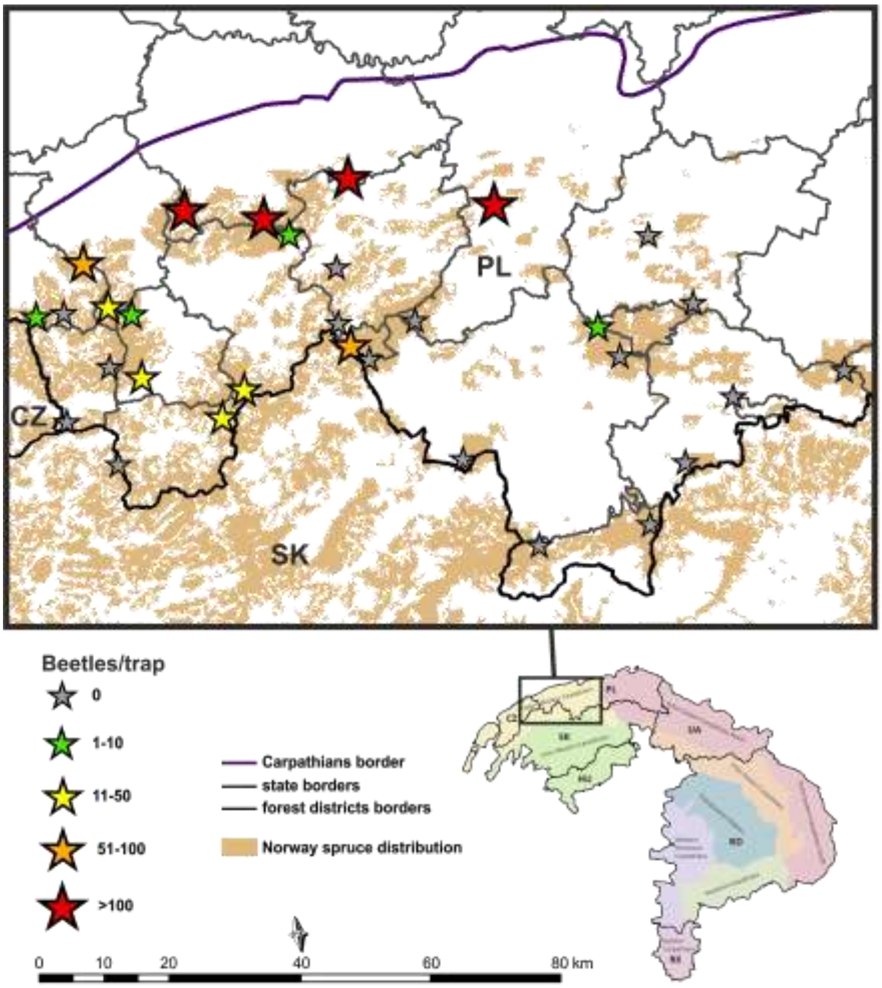
4.2.4.1 Současné rozšíření a monitoring Lýkožrouta severského (Ips duplicatus) v Karpatech

Ips duplicatus je pravidelně sledován a vyskytuje se po celé České republice v nadmořské výšce do 650 m n.m. od roku 1997. Největší odchyty i škody byly zpravidla zaznamenány v severovýchodní a východní části země (severní Morava a Slezsko), což je centrum výskytu *I. duplicatus* (Obr. 4.4). I na Slovensku je výskyt *I. duplicatus* potvrzen již od roku 1997, kdy byli brouci zachyceni ve vyšších počtech během sledování v severozápadní části země (Turčáni et al. 2001). Tento druh se šíří na východ a na jih od hraničních oblastí Slovenska (Vakula et al. 2009), což potvrzuje jeho migraci ze sousedních států. V posledních deseti letech se tento invazivní druh stává hlavním hmyzím škůdcem ve smrkových lesích slovenských Karpat (Vakula et al. 2013). *I. duplicatus* je monitorován za použití feromonových lapačů do 900 m n.m. Podle výsledků monitoringu se tento druh v současné době vyskytuje především ve smrkových lesích centrální části Západních Karpat (Tatry a Fatra), nejvíce postiženými oblastmi jsou okresy Kusycké Nové Mesto, Žilina, Bytča a Považská Bystrica (Obr. 4.4).



Obr. 4.4 Výsledky monitoringu *Ips duplicatus* na Slovensku a České republice v období 2009-2011

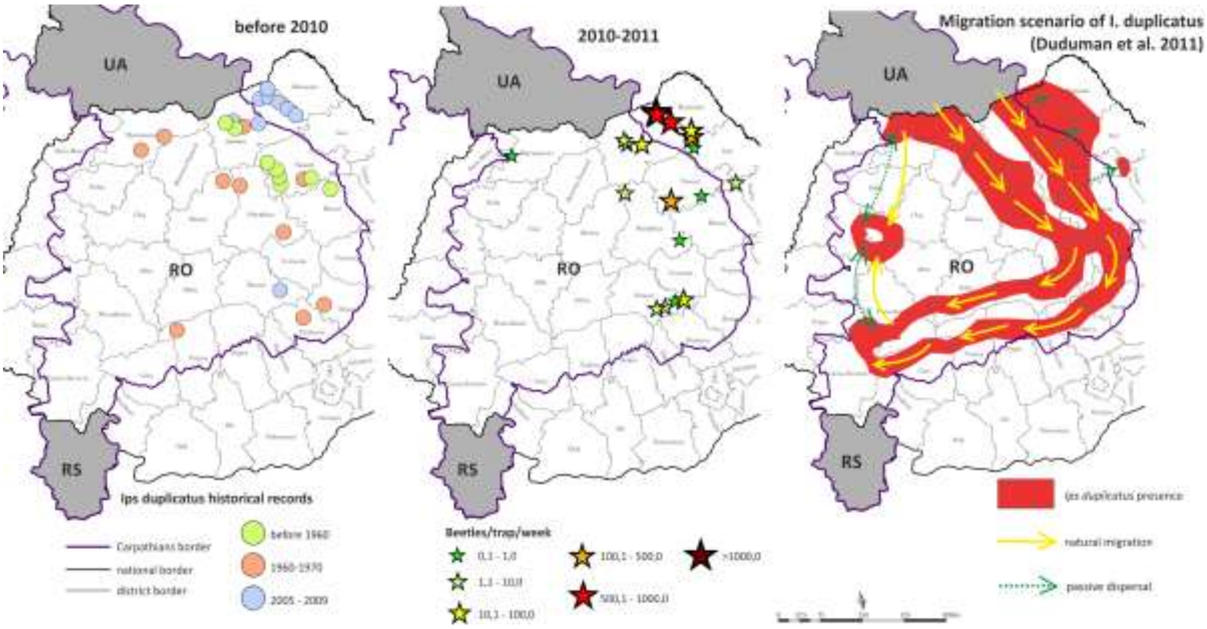
V jižním Polsku byla v celé oblasti polských Karpat zřízena v letech 2001-2002 monitorovací síť pro výskyt *Ips duplicatus*. Celkem bylo monitorováno 70 lokalit s nadmořskou výškou nad 500 m (Grodzki 2003). *I. duplicatus* byl odchycen na 17 místech lokalizovaných hlavně v západních Karpatech (Obr. 4.5).



Obr. 4.5 Výskyt *Ips duplicatus* v Polské části Karpat na základě monitoringu v letech 2001 a 2002 (podle Grodzkiho 2003)

V rumunských Karpatech byl *I. duplicatus* nalezen téměř v celé oblasti rozšíření smrku (Obr. 4.6). V roce 2010 byla přítomnost monitorována pomocí feromonových lapačů na pěti lokalitách a výzkum pokračoval v roce 2011 na třiceti místech distribuovaných na většině území rumunských Karpat. Jedinci *I. duplicatus* byli zachyceni na většině plochách, ale pouze do nadmořské výšky 1000 m n.m.

Přestože v literatuře neexistuje žádný záznam o výskytu *I. duplicatus* na území Ukrajiny a Srbska, v ukrajinské části Karpat se tento škůdce s největší pravděpodobností vykytuje, jelikož se logicky šíří mez Polskem a Rumunskem podél Karpatského hřbetu.



Obr. 4.6 Výsledky monitoringu I. duplicatus v Rumnské části Karpat před rokem 2010 (levý obrázek), mezi lety 2010-2011 (uprostřed) a a pravděpodobný průběh migrace (podle Dudumana et al. 2011)

4.2.4.2 Výskyt Ips duplicatus v horských polohách Karpat

V rámci monitoringu je *I. duplicatus* pravidelně odchytáván ve středních polohách s nadmořskou výškou do 600 m n.m. (Holuša et al. 2006) a ve vyšších nadmořských výškách Západních Karpat je jeho přítomnost potvrzena pouze ve výjimečných případech (Holuša 2004). Tento druh dosud nebyl nalezen uvnitř rozsáhlých horských pásem. Z tohoto důvodu byly studovány dvě lokality v Moravskoslezských Beskydech a Hrubém Jeseníku, které se nachází v horách dosahujících výšek 1000 m n.m. Výsledky této studie jsou uvedeny v publikaci Holuša et al. 2013 (Kapitola 5.3) a sloužily jako jeden z důležitých podkladů pro upřesnění a definici výškového limitu výskytu *I. duplicatus* v Karpatech (viz. následující kapitola).

4.2.4.3 Hodnocení vlivu změny klimatu na voltinismus Ips typographus a Ips duplicatus

Analýza předpokládaného vývoje populací lýkožrouta smrkového a lýkožrouta severského byla založena na modelu PHENIPS – Komplexním fenologickém modelu původně navrženém pro lýkožrouta smrkového (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vzduchu den nástupu napadení a průměrná teplota kůry rychlost vývoje jednotlivých vývojových stadií. Teplotní limity pro jednotlivá stadia byly určeny na základě práce Wermelinger a Seifert (1998). Přestože je v porovnání s lýkožroutem smrkovým lýkožrout severský menším druhem (Pfeffer 1955) a pro vývoj by mu mohly stačit menší kumulativní teploty, v podmínkách střední Evropy *I. duplicatus* zpravidla kopíruje fenologický model *I. typographus* (Holuša et al. 2012). Hlavním rozdílem je fakt, že se *I. duplicatus* nevyskytuje ve vysokých nadmořských výškách (Holuša et al. 2010), ale preferuje polohy do 800 m n.m. (Holuša et al. 2013). Pro definování výškového limitu byla použita data z odchytů ve feromonových lapačích. V západních Karpatech byly lapače umístěny v pravidelných 100 metrových intervalech na hoře Ostrý (Moravskoslezské Beskydy) v letech 2002 a 2003 (Holuša 2004), pro východní Karpaty byly použity výsledky studie Duduman et al. 2011. Na základě výsledků měření byl výškový limit výskytu *I. duplicatus* stanoven na 800 m n.m. pro západní a 1 000 m n.m. pro východní Karpaty. Výsledné projekce byly publikovány formou 2 souborů certifikovaných map (Příloha č. 1,2).

4.2.4.4 Současné rozšíření a dynamika populací bekyně velkohlavé pro jednotlivé země v Karpatech

Byly získány historické záznamy o škodách (defoliované ploše lesa) za období 1947 – 2013 pro sedm zemí Karpatského regionu (Česká republika, Slovensko, Polsko, Maďarsko, Rumunsko, Ukrajina a Srbsko). Získané údaje, dynamika populací a hlavní oblasti gradací jsou blíže popsány v publikaci Hlásny et al. 2016 (Kapitola 5.4). Zjištěné údaje o gradacích byly použity pro analýzu periodicity gradací, trendy v rozsahu poškození a jejich odlišnosti v rámci jednotlivých států. Dále bylo provedeno hodnocení synchronizace gradací v celokarpatském regionu. Získané statistické parametry (především periodicita gradací) byly použity při tvorbě prognostického modelu. Veškeré uvedené postupy jsou rovněž blíže popsány v publikaci Hlásny et al. 2016 (Kapitola 5.4).

4.2.4.5 Změny v potenciálních oblastech přemnožení bekyně velkohlavé

Změny v potenciálních oblastech přemnožení byly hodnoceny na základě modelu navrženého Hlásnym a Turčánim (2009). Byla použita Kanonická korespondenční analýza pro identifikaci environmentálních proměnných kontrolujících abundanci bekyně velkohlavé. Analýza prokázala positivní korelaci s teplotou vzduchu a zastoupením dubu v porostu (Hlásny a Turčáni 2009). Vážený průměr těchto proměnných (ve formě map), přepočítaný na škálu 0-1, byl použit pro identifikaci porostů potenciálně vhodných pro gradaci populací bekyně velkohlavé jak v současném, tak i budoucím klimatu. Váhy jednotlivých proměnných byly ustanoveny na 0,4 (pro zastoupení dubu) a 0,6 (pro teplotu vzduchu). Tímto způsobem byly získány mapy zobrazující gradační potenciál bekyně na území Karpat, dosahujících hodnot 0-1. Prahová hodnota 0,8 byla použita pro identifikaci potenciálních oblastí gradace. Výsledné projekce byly publikovány formou souboru certifikovaných map (Příloha č. 3).

4.2.5 Implementace vlivu škodlivých činitelů v modelu Sibyla a jeho využití při hodnocení vývoje lesních ekosystémů

Část výsledků zaměřena na hodnocení vlivu disturbancí na les a s lesem související ekosystémové služby byla realizována s využitím modelu Sibyla na území Západních Karpat (Nízké Tatry, Kozie Chrbty). Tyto studie zároveň vytvořily východiska pro formulaci doporučení pro management lesa v podmínkách změny klimatu. Souhrnné výsledky byly publikovány v pracích Hlásny et al. (2017a,b; Kapitola 5.5 a 5.7), kterých je doktorand spoluautorem. Součástí řešení byla inovativní úprava kalamitního modulu modelu Sibyla a zlepšení schopnosti reprodukovat charakteristickou ohniskovou dynamiku napadení porostů lýkožroutem. Zároveň byl vyhodnocen vliv zavedení tohoto algoritmu na simulovanou produkci a vývoj několika ukazatelů druhové a strukturální diverzity lesních porostů s dominantním zastoupením smrku. Tyto výsledky byly publikovány v práci Trombik et al. (2016; Kapitola 5.6).

Při implementaci disturbančního režimu do modelu Sibyla byl použit přístup založený na pravděpodobnosti přežívání jednotlivých druhů dřevina jejich věkových stupňů (tzv. survival probabilities). V rámci publikace Hlásny et al. 2014 (Kapitola 5.8) byly funkce pravděpodobnosti přežívání významných dřevin odvozené na základě dat lesní hospodářské evidence Slovenské republiky za období 1990-2010, které zahrnují údaje o nahodilých těžbách v důsledku všech relevantních disturbančních činitelů a všech hlavních dřevin.

Simulace dynamiky a růstu lesa byly prováděny pomocí modelu Sibyla (Fabrika a Ďurský 2005). Jedná se o empirický stromový distančně závislý hybridní model konstruovaný na bázi modelu SILVA (Pretzsch et al. 2002). V současnosti růstový simulátor Sibyla disponuje integrovaným disturbančním modulem. Modul umožňuje definovat v čase se měnící pravděpodobnost výskytu vybraných škodlivých činitelů. Pravděpodobnost výskytu disturbančního činitele lze definovat pro 5-leté periody a je stochasticky aplikována v průběhu simulace. Protože pravděpodobnost přežívaní je definována na úrovni porostu a druhu dřeviny, nelze za pomoci integrovaného modulu aplikovat odlišné pravděpodobnosti pro jednotlivé stromy v různověkých porostech. Z tohoto důvodu bylo přistoupeno k vývoji vlastního softwarového řešení kalamitního modulu, jakož i jeho parametrizace.

4.2.6 Syntéza poznatků a návrh doporučení pro management škůdců

Vyhodnocení klimatické exponovanosti Karpat, fluktuačních cyklů nejvýznamnějšího defoliátora v regionu, bekyně velkohlavé, obeznámení se s problematikou invazních škůdců formou studie ohledně lýkožrouta severského a realizace komplexních studií ohledně vývoje lesa vystaveného disturbancím a změně klimatu umožnily formulovat relativně ucelené opatření ohledně adaptace lesů na změnu klimatu. Tento systém byl nejprve publikován ve studii Hlásny et al. 2014 (Kapitola 5.8). Doporučení pro management lesa byla dále formulována v pracích realizovaných s využitím modelu Sibyla ((2017a,b; Kapitola 5.5 a 5.7). Metodický postup formulace opatření spočíval v rozsáhlém studiu domácí i zahraniční literatury, na základě které byly formulovány obecné principy adaptace pro jednotlivé oblasti managementu lesa (pěstování, těžba, ochrana, lesní infrastruktura, monitoring apod.). Následně byly tyto obecné principy zpřesněny s ohledem na přírodní podmínky střední Evropy a výsledky regionálních studií, včetně těch, které tvoří součást této práce. Výsledky, na kterých se doktorand podílel, přispěly zejména k formulaci doporučení z oblastí ochrany lesa a monitoringu škůdců.

5. Výsledky

Předkládaná dizertační práce je postavena na 7 článcích a 3 souborech certifikovaných map, zabývajících se výsledky analýz a interpretací výsledků jednotlivých parciálních cílů. Na všechny tyto práce je odkazováno v rámci textu předchozích kapitol. Problematikou dat o distribuci a dřevinném složení lesa a hodnocení jejich přesnosti se zabývá publikace:

Kapitola 5.1) TROMBIK, J. – HLÁSNY, T. (2013) Free European data on forest distribution: overview and evaluation. *Journal of Forest Science,* roč. 59, č. 11, s. 447-457. ISSN: 1212-4834.

použitím získaných klimatických dat a hodnocením očekávaných změn a klimatickou exponovaností regionu Karpat jsou hlavním tématem publikace:

Kapitola 5.2) HLÁSNY, T. – TROMBIK, J. – DOBOR, L. – BARCZA, Z. – BARKA, I. (2016a) Future climate of the Carpathians: climate change hot-spots and implications for ecosystems. *Regional Environmental Change,* roč. 16, č. 5, s. 1495-1506. ISSN: 1436-3798.

2 publikace a 3 soubory map (předložené v Přílohách této práce) se zabývají problematikou výskytu a časoprostorové dynamiku vybraných biotických škodlivých činitelů v Karpatech:

Kapitola 5.3) HOLUŠA, J. – LUKÁŠOVÁ, K. – TROMBIK, J. (2013) The first record of *Ips duplicatus* (Coleoptera: Curculionidae, Scolytinae) infestations in central european inner mountains. *Scientia Agriculturae Bohemica,* roč. 44, č. 2, s. 97-101. ISSN: 1211-3174.

Kapitola 5.4) HLÁSNY, T. – TROMBIK, J. – HOLUŠA, J. – LUKÁŠOVÁ, K. – GRENDÁR, M. – TURČÁNI, M. – ZÚBRIK, M. – TABAKOVIĆ-TOŠIĆ, M. – HIRKA, A. – BUKSHA, I. – MODLINGER, R. – KACPRZYK, M. – CSÓKA, G. (2016b) Multi-decade patterns of gypsy moth fluctuations in the Carpathian Mountains and options for outbreak forecasting. *Journal of Pest Science,* roč. 89, č. 2, s. 413-425. ISSN: 1612-4758.

Příloha 1) HLÁSNY, T. – TROMBIK, J. – HOLUŠA, J. – LUKÁŠOVÁ, K. (2013) Soubor map: Dopad klimatických změn na populace lýkožrouta severského (*Ips duplicatus,* Coleoptera: Curculionidae) v Karpatech: Vliv na distribuci a populační dynamiku. Číslo certifikátu 82918/2013-MZE-16222/MAPA604, Ministerstvo zemědělství, Těšnov 65/17, Praha 1, 11705.

Příloha 2) TROMBIK, J. – HLÁSNY, T. – HOLUŠA, J. (2013) Soubor map: Dopad klimatických změn na populace lýkožrouta smrkového (*Ips typographus,* Coleoptera: Curculionidae) v Karpatech: Vliv na distribuci a populační dynamiku. Číslo certifikátu 82922/2013-MZE-16222/MAPA605, Ministerstvo zemědělství, Těšnov 65/17, Praha 1, 11705.

Příloha 3) HLÁSNY, T. – TROMBIK, J. – LUKÁŠOVÁ, K. (2013) Soubor map: Dopad klimatických změn na populace bekyně velkohlavé (*Lymantria dispar* Lepidoptera: Lymantriidae) v Karpatech: Vliv na distribuci a populační dynamiku. Číslo certifikátu 82916/2013-MZE-16222/MAPA603, 2013, Ministerstvo zemědělství, Těšnov 65/17, Praha 1, 11705.

využitím získaných poznatků o vlivu škodlivých činitelů a jejich implementací vlivu v modelu dynamiky lesa s následným hodnocením vývoje lesních ekosystémů se zabývají 3 publikace:

Kapitola 5.5) HLÁSNY, T. – BARKA, I. – KULLA, L. – BUCHA, T. – SEDMÁK, R. – TROMBIK, J. (2017a) Sustainable forest management in a mountain region in the Central Western Carpathians, northeastern Slovakia: the role of climate change. *Regional Environmental Change,* roč. 17, č. 1, s. 65-77. ISSN: 1436-3798.

Kapitola 5.6) TROMBIK, J. – BARKA, I. – HLÁSNY, T. (2016) Effect of different tree mortality patterns on stand development in the forest model SIBYLA. *Lesnicky časopis (Forestry Journal),* roč. 62, č. 2016, s. 173-180. ISSN: 0323-1046.

Kapitola 5.7) HLÁSNY, T. – BARKA, I. – ROESSIGER, J. – KULLA, L. – TROMBIK, J. – SARVAŠOVÁ KVIETKOVÁ, M. – BUCHA, T. – KOVALČÍK, M. – ČIHÁK, T. (2017b) Conversion of Norway spruce forests in the face of climate change: a case study in Central Europe. *European Journal of Forest Research,* roč. 136, č. 5-6, s. 1013-1028. ISSN: 1612-4669.

formulací možných opatření adaptace lesů na změnu klimatua a doporučení pro management lesa je věnována práce:

Kapitola 5.8) HLÁSNY, T. – CSABA, M. – SEIDL, R. – KULLA, L. – MERGANIČOVÁ, K. – TROMBIK, J. – DOBOR, L. – BARZCA, Z. – KONOPKA, B. (2014) Climate change increases the drought risk in Central European forests: What are the options for adaptation? *Lesnicky časopis (Forestry Journal),* roč. 60, č. 1, s. 5-18. ISSN: 0323-1046.

5.1 Free European data on forest distribution: overview and evaluation.

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Free European data on forest distribution: overview and evaluation

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ABSTRACT: A growing need for the evaluation of prospects and sustainability of forest resources calls for the availability of harmonized data on forest distribution. We described and evaluated nine datasets providing such information: Corine LandCover, four European forest maps and four tree species distribution maps. Apart from providing a condensed overview of these datasets, we focused on the match between selected forest maps and forest management plans (FMPs) of Slovakia, which can be thought of as highly accurate information on forest distribution. The degree of match between forest and species area, within 306 forest administrative districts of Slovakia, was used as an indicator of accuracy. In addition, the match between the total forest and species area in Slovakia, given by FMPs and by evaluated datasets, was addressed. We found a high degree of match for the datasets on forest distribution (R-square 0.77–0.93, depending on the dataset), as well as strong agreement in total forest area (± 5%). Both indicators are worse in the case of forest type evaluation (coniferous and broadleaved). Poor results were obtained for tree species maps, which under- or overestimated species areas by tens of per cent, although differences were highly variable among species. The obtained results are valid mainly for temperate forests.

Keywords: tree species distribution; data quality; forest management plans; accuracy assessment

An increasing number of studies focus on the transboundary or even pan-European evaluation of forest resources (e.g. Badea et al. 2004; Percy, Ferreti 2004). These activities are often limited by a lack of suitable data on forest distribution for such large-scale use. In fact, forest management plans of many European countries contain high-quality forestry data, including a range of stand and site variables, with fine spatial resolution. However, despite the recent effort of most countries to establish legislation on free access to public data, access to national or institutional databases is often limited, and such data are not obviously available for research or commercial activities. Recently, climate change-related research has become an important area to suffer from the low quality of forestry data, which lags behind the continuously increasing resolution of climate models. In addition, forest area is one of the indicators for sustainable forest management in Europe (MCPFE 2003), and information on tree species distribution is important in the assessment of forest-related biodiversity, in connection with the United Nations Convention on Biological Diversity and affiliated European processes (Tröltzsch et al. 2009). The development of European forest maps is also needed for protection and conservation, carbon storage evaluation or forest planning (Schuck et al. 2003). For these reasons, several initiatives have been taken to develop unified datasets on forest distribution in Europe. The availability of such datasets may lead to improved forest resource modelling, able to deal with high-resolution forest diversity in Europe (Brus et al. 2011). Undoubt-

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edly, CORINE Land Cover (EEA 1994, 2006 a,b) has been recognised as an extremely useful dataset, and has been used in dozens of studies since its first release (e.g. Sifakis et al. 2004; Traustason, Snorrason 2008; Mag et al. 2011). Later, an increase in the quality and availability of remote sensing data, as well as methodological advances in the processing of spatial data, led to the development of numerous forest maps with different geographical coverage, providing diverse information on forests. In addition to forest and forest-type maps, maps of tree species distribution have been found to be extremely important for forest resources evaluation, biodiversity assessment and forest planning (e.g. Tröltzsch et al. 2009; Brus et al. 2011). In addition, there are specialized forest maps, such as forest management maps by Hengeveld et al. (2012), forest biomass maps by Barredo et al. (2012), or various global forest and landcover maps (e.g. Defries et al. 2000; Bartholomé, Belward 2005; Ahlenius 2012), which are not, however, addressed in this study.

Despite the availability of numerous forest maps with European coverage, a critical evaluation of their quality and suitability for various objectives is missing. For this reason, this article aims to describe the freely available data on forest distribution, with mostly pan-European coverage, and evaluate the limits and assets of such data. In particular, we focused on:

- surveying the sources of freely available data on forest distribution in Europe;
- evaluating the content, quality, accuracy, coverage and other attributes of such data;
- evaluating the quality of selected datasets on forest distribution in Europe, on the basis of their match with forest management plans (FMPs) of Slovakia.

We hypothesize that datasets containing information on forest distribution and the distribution of forest types (broadleaved, coniferous and mixed) could show a very good match with the FMPs. This assumption is grounded in the fact that currently available satellite imagery and classification algorithms, which are used for the development of most of the addressed dataset, allow for the highly accurate delineation of forest areas (e.g. Kempeneers et al. 2011; Potapov et al. 2011). On the other hand, we suppose lower quality of data on tree species distribution, in terms of their match with FMPs. This assumption issues from the fact that the spatial interpolation of point data on the species proportion, which is generally applied for the development of evaluated datasets, could produce largely uncertain results, depending on the spatial density of data and the pattern of spatial autocorrelation specific to analysed species. In addition, we assume that maps of species with scattered distribution may have poorer quality when compared to maps of species with contagious range.

DATA AND METHODS

Evaluated datasets

Two groups of forest maps have been evaluated. The first group contains maps on the distribution of category 'forest', which is divided further in some datasets into subcategories coniferous, broadleaved and mixed. CORINE Land Cover data (EEA 1994, 2006 a,b) and four European forest maps were included into this group (Schuck et al. 2002; Pekkarinen et al. 2009; Gunia et al. 2011; Kempeneers et al. 2011). The second group contains maps providing information on forest tree species distribution such as EUFORGEN maps (EUFORGEN 2009), tree species distribution maps based on the Forest Focus data (FORESTMOD 2013), and two results of statistical mapping of tree species distribution in Europe (Tröltzsch et al. 2009; Brus et al. 2011) were included into this group.

CORINE Land Cover (CORINE – EEA 1994)

The CORINE (**Coor**dinate **In**formation on the **En**vironment) database is a pan-European land cover map, developed by the European Environmental Agency (EEA) in cooperation with national partner institutions. The dataset covers the 27 countries of the European Union (EU27), as well as Albania, Bosnia and Herzegovina, Croatia, Macedonia, and Liechtenstein. Three land-cover categories define the forests: broadleaved (proportion > 75%); coniferous (> 75%); and mixed forests (remaining forest land) (EEA 1994). The dataset was developed on the basis of multispectral satellite imagery acquired by Landsat and Spot instruments, and additional national data such as topographic maps, thematic maps, statistical information and aerial photographs (EEA 1994, 2006 a,b), with the minimum mapping unit of 25 ha. The dataset is available through the web portal of the EEA as raster files (TIFF format with a resolution of 100 and 250 m) and vector files (ESRI shp file). CORINE 2006 is currently the latest update; the version available in ESRI shp file format was used in this study.

Forest Map 2000 (FMAP 2000; Pekkarinen et al. 2009)

FMAP 2000 contains the information on forest and non-forest categories, derived from 415 Landsat ETM+ satellite scenes and CORINE Land Cover 2000, with a spatial resolution of 25 m. The map covers the EU-27 countries, Norway, Switzerland, Lichtenstein, Albania, Croatia, Macedonia, Montenegro and Serbia. The map's overall point-level agreement exceeds 80%, and it approaches 90% in Central Europe. A comparison with the country-level forest area statistics shows that, in most cases, the difference between the forest proportion of the derived map and that computed from the published forest area statistics is below 5% (Pekkarinen et al. 2009). The maps can be downloaded from the website of the Joint Research Centre of the European Commission (http://forest.jrc.ec.europa.eu) as raster data (TIFF format).

Forest map 2002 (EFMAP 2002; Schuck et al. 2002)

EFMAP 2002 represents the proportion of coniferous and broadleaf forests per land area in a 1 × 1 km pixel resolution. The map was derived from NOAA-AVHRR satellite imagery, and calibrated to conform to statistical information on forest area, such as national inventory reports and data from international data-collection processes of the United Nations Economic Commission for Europe/Food and Agriculture Organisation (UNECE/FAO 2000; Päivinen et al. 2001). The difference between the map and inventory statistics varies around ± 5% (higher in the coastline and small island area) (Schuck et al. 2003). EFMAP 2002 includes all European countries except for Cyprus and Turkey. The map can be downloaded from the European Forest Institute (EFI) website (http://www.efi.int/projects/euromap/phase2/register.php), as raster data (IMAGINE Image format).

Forest Map 2006 and Forest Type Map 2006 (FTYP 2006; FMAP 2006; Kempeneers et al. 2011)

The FMAP 2006 contains forest, non-forest and water categories, while the FTYP 2006 contains broadleaved and coniferous categories. The resolution of both datasets is 25 m. The maps were produced using IRS-LISS-3 and SPOT4/5 satellite scenes, acquired in 2006. Multitemporal information obtained from the MODIS sensor (NASA) was added to improve the classification. FMAP 2006 and FTYP 2006 cover the same area as FMAP 2000, but they also include Turkey. The result can be downloaded from the EC-JRC website (http://forest.jrc.ec.europa.eu) as raster data (TIFF format).

Forest map 2011 (EFMAP 2011; Gunia et al. 2011)

EFMAP 2011 represents the modified version of FMAP 2006 (Kempeneers et al. 2011), which was aggregated from the original 25 m spatial resolution to 1 km, by summing up the forest area for each 1 km pixel (the proportion of forests is given). Forest share estimates taken from the 1 km resolution EFMAP 2002 (Schuck et al. 2002) have been used to extend the map up to the Ural Mountains, covering Belarus, Ukraine, Moldova and the European part of the Russian Federation. The map can be downloaded from the EFI website (http://www.efi.int/projects/euromap/phase2/register.php) as raster data (IMAGINE Image).

Tree species distribution maps 1 (EUFORGEN – EUFORGEN 2009)

The European Forest Genetic Resources Programme (EUFORGEN) produced a series of pan-European maps of forest tree species distribution. The maps were produced by members of the EUFORGEN Networks and other experts, on the basis of diverse information sources. The dataset contains polygonal data with the area of occurrence of 34 tree species across Europe. The dataset is available through the EUFORGEN web (http://www.euforgen.org/distribution_maps.html) as ESRI shape files (shp). The maps are updated irregularly.

Tree species distribution maps 2 (TMAP 2009; Tröltzsch et al. 2009)

TMAP 2009 is based on tree species information from plot data of the ICP (International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) Forests, with the spacing of 16 × 16 km, which is combined with other spatial and statistical information. The point data were interpolated using the kriging method, and produced maps were scaled and calibrated to make the maps correspond to the Forest Map of Europe, version 2002 (Schuck et al. 2002) at a pixel level, and to national forest inventory statistics at regional or national levels (Tröltzsch et al. 2009). The outputs are pan-European maps with a resolution of 1 km, containing proportions of the main tree species groups as a percentage of the total land area. The maps were developed for pine, spruce, fir, birch, beech and oak species groups. All remaining species were grouped into categories 'other coniferous' and other broadleaf. The maps cover the entire Europe except for countries for which ICP and/or detailed national forest inventory were not available (e.g. Macedonia, Cyprus, parts of Russia, Andorra, Liechtenstein).

Tree species distribution maps 3 (TMAP 2011; Brus et al. 2011)

TMAP 2011 contains maps with a proportion of 18 tree species in a 1 × 1 km resolution grid. The ICP-Level-I plot data on tree species distribution (6,238 plots) and National Forest Inventory data of eighteen countries (335,360 plots, Nabuurs 2009) were used for the development of this dataset. In areas with national forest inventory data, species area proportions were obtained by compositional kriging. For the rest of Europe, a multinomial logistic regression model was used, using various abiotic factors as predictors (soil, biogeographical zones, climate data). The regression results were scaled to fit NUTS-II forest inventory statistics and the European Forest Map, according to TRÖLTZSCH et al. (2009) and SCHUCK et al. (2002). Maps of 20 tree species are available in the dataset. The accuracy of produced maps was highly variable, depending on the species; the overall accuracy equals 43%. In areas with NFI plot data, the accuracy was 57%, and outside these areas 33%. GIS data are available for download from the EFI website (http://www.efi.int/projects/tree-species-map/register.php) as raster files (ESRI file geo-database).

Tree species distribution maps 4 (FMOD; FORESTMOD 2013)

The map contains information on tree species proportions in a 1-km resolution grid. The Forest Focus database (Forest Focus 2003) containing information about the tree species composition on the basis of a systematic network of observation points and observation plots was the main source of data. The point data were interpolated and then scaled to FMAP 2000 (PEKKARINEN et al. 2008). The results contain the distribution of 24 tree species. The maps cover the EU-27, as well as Norway, Switzerland, Lichtenstein, Albania, Croatia, Macedonia, Montenegro and Serbia. The maps can be acquired using the FORESTMOD map viewer (http://forest.jrc.ec.europa.eu/efdac/applications/species-distrbution/) as raster files (TIFF format).

Modification of low-resolution raster data

Some of the datasets described above contain data in a 1-km resolution grid. To improve the visual and analytical properties of these data, we applied the following modification. The original grid data were transformed to vector format, and the produced polygons were intersected with forest polygons from CORINE Land Cover data. Then, forest cells, or their parts lying outside the forest area specified by CORINE Land Cover, were removed. In the case of tree species maps, CORINE categories 'Coniferous' and 'Mixed' were used to modify the coniferous species, and CORINE categories 'Broadleaved' and 'Mixed' were used to modify the broadleaved species. EFMAP 2002 and 2011, TMAP 2011 and FMOD datasets were modified using this methodology. The effect of such modification on the map accuracy was evaluated.

Forest management plans of Slovakia

We evaluated the accuracy of selected freely available data using the Slovakian FMPs (National Forest Centre, Slovakia, internal data), which represent the information on forest tree species distribution, independent of all evaluated data sources. The information on tree species proportions in the FMPs is associated with forest subcompartments, of the average size approximately 5 ha. This data can be a priori thought of as more accurate when compared with the evaluated datasets, because FMPs are compiled on the basis of regular 10-year step field surveys, i.e. one tenth of country's forested area is updated annually. This implies that used FMPs refer to the period 2003–2012 (the analysis was run in 2013). This fact introduces certain temporal inconsistency into the analysis, as well as temporal mismatch between the FMPs and evaluated datasets on forest distribution. Considering the scale which the analysis focuses on and relatively low forest dynamics at this scale, such inconsistency cannot be expected to affect the results.

Accuracy assessment

As most of the evaluated datasets can be expected to have a relatively low informative value at the stand scale, owing to the inherent effect of their low spatial resolution, we focused our evaluation on the scale of 306 forest administrative districts (FADs) of Slovakia, with an average size of 150 km^2. The accuracy assessment was focused on a comparison of the extent of forest categories in the evaluated datasets with data from FMPs of Slovakia within FADs.

To facilitate this analysis, the map of FADs was transformed from the national coordinate system (S-JTSK Krovak) to Lambert Azimuthal Equal Area (LAEA) projection on the ETRS ellipsoid using the ArcInfo GIS (ESRI 2010) tools; ETRS LAEA was the system of all evaluated datasets. The error due to this transformation is not expected to affect the analysis. FMPs were not transformed, and forest, forest type and species areas within FADs were calculated in the original national coordinate system (S-JTSK Krovak).

In the case of forest type evaluation (coniferous, broadleaved, mixed), species proportions in FMPs were classified so as the definition of a given forest type corresponded with the definition of this forest type in the evaluated dataset. No limit was imposed on stand density, age and other attributes in the FMPs, and all forest compartments were used in the analysis.

Correlation analysis was applied to describe the relationship between these variables, and to evaluate the strength of correlations using the R-square. The analysis was performed separately for FADs, with mean elevation above and below 600 m a.s.l., as well as for all FADs regardless of their elevation. In addition, a comparison of total forest, forest type and species areas, given by

FMPs and evaluated datasets, was made. In the case of tree species maps, we focused on selected temperate forest tree species with contagious and scattered distribution: European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and Silver fir (*Pinus sylvestris*).

RESULTS

Summary information on all addressed datasets is given in Table 1. Correlation analysis of forest and forest type areas within FADs indicated remarkable differences between the match of FMPs and evaluated datasets (Table 2). FMAP 2000 with the resolution of 25 × 25 m performed best out of all datasets (R-square 0.93 in all FAD), and showed equally high R-squares in both elevation zones addressed (below and above 600 m a.s.l.). CORINE Land Cover reached similar accuracy. However, it slightly outperformed the FMAP 2000 in FADs at elevations below 600 m a.s.l. (R-square 0.97).

FMAP 2006 with 25-m resolution and EFMAP 2011 with 1-km resolution showed balanced, and

Table 1. Basic properties of forest maps addressed in this study; map abbreviations are explained in the text

Dataset	Format	Resolution	Coverage	Main data sources	Forest categories	Attribute	Reported accuracy
CORINE 2006	raster, vector	1 : 100,000; 100 × 100 m; 250 × 250 m	EU-27, Albania, Bosnia and Herzegovina, Croatia, Macedonia, and Liechtenstein	Landsat and Spot satellites, national topographic and thematic maps, statistical information and aerial photographs	broadleaved, coniferous, mixed	presence/absence	> 85%
EFMAP 2002	raster	1 × 1 km	all European countries from Portugal to Ural Mts., except Cyprus and Turkey	AVHRR-NOAA; forest inventory statistics	forest/non-forest; broadleaved; coniferous	forest or forest type proportion	variable, overall ± 5%, lower accuracy in the coastline area
FMAP 2000	raster	25 × 25 m	EU-27, Norway, Switzerland, Lichtenstein, Albania, Croatia, Macedonia, Montenegro and Serbia	Landsat ETM+ imagery; Corine LandCover 2000	forest/non-forest	presence/absence	> 80%
FMAP 2006 FTYP 2006	raster	25 × 25 m	EU-27 and Norway, Switzerland, Lichtenstein, Albania, Croatia, Macedonia, Montenegro, Serbia and Turkey	IRS-LISS-3; SPOT4/5; Corine LandCover 2000	forest/non-forest; broadleaved; coniferous	presence/absence	> 80%
EFMAP 2011	raster	1 × 1 km	same as FMAP 2006; added Belarus, Moldova, Ukraine and Russian Federation (from SCHUCK et al. 2002)	IRS-LISS-3; SPOT4/5; Corine LandCover 2000 and AVHRR-NOAA; forest inventory statistics	forest/non-forest	forest proportion	> 80%; lower for Belarus, Ukraine, Moldova and Russia
EUFORGEN	vector	unspecified	all European countries; except Cyprus, Turkey and Russia	national experts; bibliography	34 forest tree species	presence/absence	not specified
TMAP 2009	raster	1 × 1 km	Pan-European area except Macedonia, Cyprus, parts of Russia other than the Leningrad and Kaliningrad regions, Andorra and Liechtenstein	ICP Level 1 plots; European Forest Map; Forest inventory statistics; selected environmental variables	6 forest tree species	species proportion	variable between the countries, correlation from cross-validation 0.2 to 0.8
TMAP 2011	raster	1 × 1 km	Pan-European area except Macedonia, Cyprus, parts of Russia other than the Leningrad and Kaliningrad regions, Andorra and Liechtenstein.	NFI plots; Forest inventory statistics; selected environmental variables	20 forest tree species	species proportion	43%, highly variable among species
FORESTMOD	raster	1 × 1 km	EU-27, Norway, Switzerland, Lichtenstein, Albania, Croatia, Macedonia, Montenegro and Serbia	FMAP 2000; Forest Focus database	24 forest tree species	species proportion	not specified, highly variable among species and locations

Table 2. R-squares calculated between areas occupied by main forest type categories within forest administrative districts in Slovakia, taken from the FMPs of Slovakia and six maps of forest distribution in Europe (CORINE – EEA 1994; FMAP 2000; EFMAP 2002; SCHUCK et al. 2002; FMAP 2006; FTYP 2006; PEKKARINEN et al. 2009; EFMAP 2011, GUNIA et al. 2011; KEMPENEERS et al. 2011)

Category	Elevation zone	FMAP		EFMAP	EFMAP			FTYP	CORINE
		2000	2006	2002	2002*	2011	2011*	2006	
Forest	all districts	0.93	0.88	0.88	0.77	0.88	0.82	–	0.89
	< 600 m a.s.l.	0.94	0.94	0.82	0.76	0.92	0.90	–	0.97
	> 600 m a.s.l.	0.94	0.87	0.93	0.83	0.88	0.80	–	0.86
Broadleaved	all districts	–	–	0.66	0.60	–	–	0.93	0.98
	< 600 m a.s.l.	–	–	0.77	0.65	–	–	0.92	0.97
	> 600 m a.s.l.	–	–	0.69	0.80	–	–	0.82	0.95
Coniferous	all districts	–	–	0.91	0.86	–	–	0.91	0.92
	< 600 m a.s.l.	–	–	0.54	0.72	–	–	0.85	0.92
	> 600 m a.s.l.	–	–	0.93	0.84	–	–	0.90	0.90
Mixed	all districts	–	–	–	–	–	–	–	0.77
	< 600 m a.s.l.	–	–	–	–	–	–	–	0.74
	> 600 m a.s.l.	–	–	–	–	–	–	–	0.77

*modification of the original dataset using CORINE Land Cover data described in the text

in the case of the latter dataset, the applied modification by CORINE Land Cover did not affect the R-square substantially. The R-square of FMAP 2006 and EFMAP 2011 at elevations < 600 m a.s.l. was equal to FMAP 2000 map performance in all districts, but at elevations > 600 m a.s.l. it was, however, weaker. EFMAP 2002 with 1-km resolution had lower accuracy as compared with FMAP 2000 (R-square 0.88 vs. 0.93 in all districts). Surprisingly, the map modification by CORINE Land Cover reduced the R-square, and it reached 0.77 in all districts. Hence, such modification is not advisable in the case of this map.

Much higher variability of R-squares was observed among datasets, forest type categories and elevation zones in the case of coniferous and broadleaved forest type classes. CORINE outperformed the EFMAP 2002 and FTYP 2006 in both coniferous and broadleaved classes (mixed is not included in the latter two datasets). A high degree of match with FMPs was found in the case of the CORINE broadleaved category (R-square 0.98 in all districts), while it reached 0.92 for the coniferous and 0.77 for the mixed categories (definition of these categories in FMPs was the same as CORINE forest classes). EFMAP 2002 was found to have the lowest performance, and its R-square

Table 3. R-squares calculated between areas occupied by three forest tree species within forest administrative districts in Slovakia, taken from the "forest management plans" of Slovakia and two maps of tree species distribution in Europe (TMAP 2011; BRUS et al. 2011; FMOD – FORESTMOD 2013)

Species	Elevation zone	TMAP 2011	TMAP 2011*	FMOD	FMOD*
European beech	all districts	0.52	0.67	0.52	0.49
	< 600 m a.s.l.	0.59	0.60	0.55	0.52
	> 600 m a.s.l.	0.53	0.82	0.50	0.55
Silver fir	all districts	0.33	0.54	0.17	0.20
	< 600 m a.s.l.	0.14	0.67	0.55	0.71
	> 600 m a.s.l.	0.40	0.46	0.07	0.08
Norway spruce**	all districts	0.83	0.85	–	–
	< 600 m a.s.l.	0.35	0.87	–	–
	> 600 m a.s.l.	0.85	0.81	–	–

*modification of the original dataset using CORINE Land Cover data described in the text, **spruce was not included in the FMOD dataset reached only 0.66 in all broadleaved districts. Better results were obtained for coniferous categories in all districts (R-square 0.91), but R-square in the elevation zone < 600 m a.s.l. was only 0.54 (improved by CORINE modification to 0.72). Modification by CORINE Land Cover did not improve the results in other cases. FTYP 2006 with 25-m resolution showed high performance in both coniferous and broadleaved categories, and R-square reached 0.93 and 0.91, respectively, in all districts. For the visual evaluation of selected datasets see Fig. 1.

The analysis of tree species maps was focused on TMAP 2011 (Brus et al. 2011) and FMOD maps (FORESTMOD 2013; Table 3), both with 1-km resolution. In contrast to the analysis of forest types, modification by CORINE resulted in substantial improvement in all three species in both datasets.

The highest degree of match with FMPs was observed in spruce from the TMAP 2011 (R-square 0.83 in all districts), though R-square in elevations up to 600 m a.s.l. was only 0.35. This value, however, increased remarkably after modification by CORINE Land Cover, and reached 0.87. A similar effect was observed in the case of Silver fir at an elevation of up to 600 m a.s.l., where the R-square reached only 0.14 in the original TMAP 2011, and 0.55 in the original FMOD. After modification, these values reached 0.67 and 0.71, respectively. In the case of beech, original TMAP 2011 reached the same R-square as FMOD (0.52). Modification by CORINE Land Cover was beneficial only in the case of TMAP 2011 (R-square 0.67), while it caused a minor worsening in the case of FMOD (R-square 0.49). Maps for Silver fir, which occurs mainly as an admixture species, showed low performance, and R-square reached 0.33 in TMAP 2011 and 0.17 in FMOD (case of all districts). A substantial effect of modification by CORINE Land Cover was observed in TMAP 2011 (R-square 0.54), while this effect was only minor in FMOD (R-square 0.2). For the visual evaluation of beech and fir distributions see Figs 2 and 3.

In addition to the presented analysis, we evaluated the match among the total area of forest, forest types and tree species, taken from the FMPs and from the evaluated datasets (presented forest and forest tree species areas are different from official national statistics, because of different methodology used in these calculations) (Table 4). Datasets providing information on forest and forest type distribution were found to correspond very well with the respective areas from FMPs, except for FMAP 2000, which overestimated the total forest area by ca 20%. Modification by CORINE Land Cover had

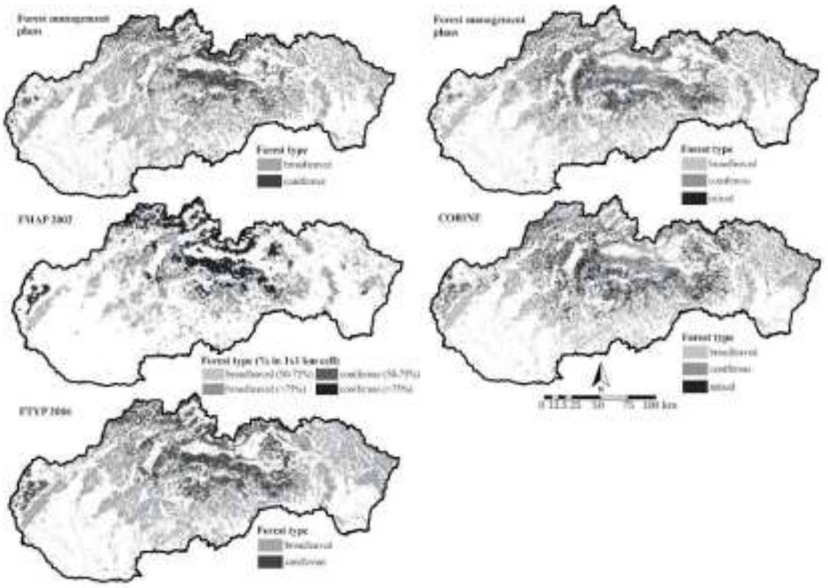

Fig. 1. Maps of forest type distribution, taken from forest management plans of Slovakia and from three freely available datasets on forest distribution in Europe

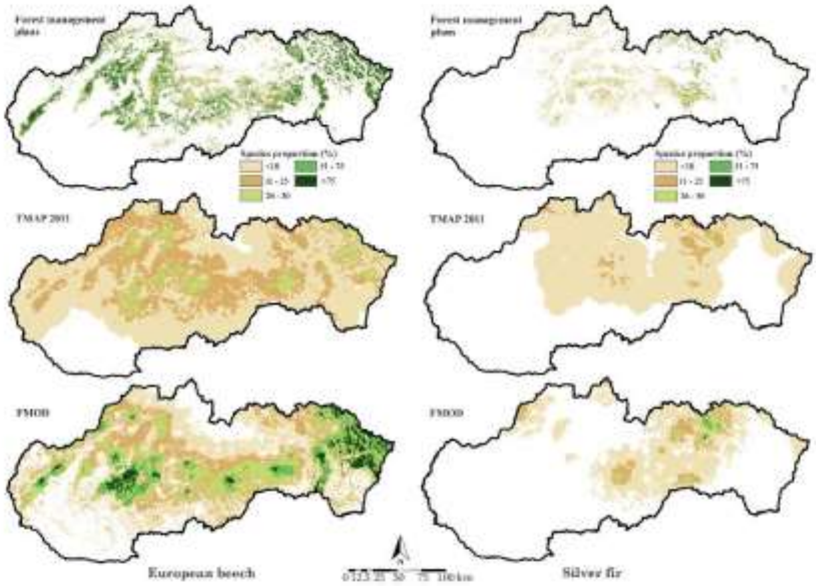

Fig. 2. Distribution maps of European beech and Silver fir, taken from forest management plans of Slovakia and two freely available datasets, based on statistical mapping

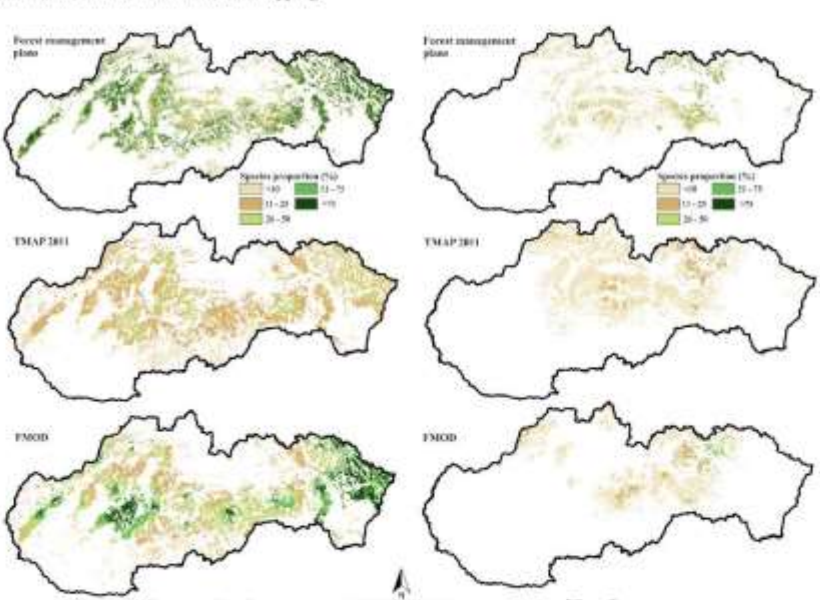

Fig. 3. Distribution maps of European beech and Silver fir, taken from forest management plans of Slovakia and two freely available datasets, based on statistical mapping, the maps were modified by CORINE Land Cover

Table 4. Comparison of areas occupied by the total forest area, forest types and three forest tree species in Slovakia, taken from forest management plans and from 8 European datasets on forest distribution

Dataset	Forest	Coniferous	Broadleaved	Mixed	*F. sylvatica*	*A. alba*	*P. abies*
FMPs (km^2)	18,272	7,288	10,683	3,636	7,687	800	6,198
FMAP 2000 (%)	+19.8	–	–	–	–	–	–
FMAP 2006 (%)	–5.3	–	–	–	–	–	–
EFMAP 2002 (%)	+1.9	–0.2	+7.6	–	–	–	–
EFMAP 2002* (%)	–33.0	–3.5	–29.4	–	–	–	–
EFMAP 2011 (%)	–0.3	–	–	–	–	–	–
EFMAP 2011* (%)	–23.4	–	–	–	–	–	–
FTYP 2006 (%)	–	–1.9	+7.0	–	–	–	–
CORINE (%)	+2.9	–3.6	–3.3	+5.0	–	–	–
TMAP 2011 (%)	–	–	–	–	–44.5	+86.9	–1.9
TMAP 2011* (%)	–	–	–	–	–70.9	–10.5	–59.2
FMOD (%)	–	–	–	–	+5.2	–22.4	–
FMOD* (%)	–	–	–	–	–31.9	–64.2	–

*modification of the original dataset using CORINE LandCover data described in the text

a detrimental effect on all maps, and the removal of parts of the forest area distributed outside the CORINE forest classes caused a substantial underestimation of the total forest area, as compared with FMPs. Poor results were obtained for tree species maps, which under- or overestimated species areas in tens of per cent in both evaluated datasets (TMAP 2011 and FMOD).

EUFORGEN maps represent another dataset containing data on the distribution of forest tree species, which has not been addressed in the previous analyses. Visual investigation of the match between several EUFORGEN maps (European beech, Norway spruce and Silver fir) and FMPs revealed erroneous geographical projection, which resulted in the shifted and distorted position of evaluated species maps. The distortion was remarkable for both beech and spruce, and increased to the south-east of Europe. Provided that this problem has been fixed, the EUFORGEN maps can be expected to match the real tree species distribution very well.

DISCUSSION AND CONCLUSIONS

This study used consistent information from several datasets which provide free access to data on forest distribution, with approximately pan-European coverage. In addition to the general description of this data, we evaluated the accuracy of selected datasets by their comparison with forest management plans of Slovakia. In line with hypotheses stated at the beginning of this study, we found a high agreement between forest management plans and maps describing forest and forest type distribution, in terms of both performed correlation analysis and comparison of the extent of total forest area in the country. Such results agree with evaluations provided by the authors of the maps, who indicate their accuracy to exceed 80% in all datasets. Our findings corroborate the validity of these evaluations, and emphasize the suitability of evaluated datasets for Central Europe. Hence, the use of these data seems advisable for most pan-European or transboundary initiatives, such as the Carpathian Initiative or the Danube Strategy. The high performance of CORINE Land Cover in all three forest types (coniferous, broadleaved, mixed), and the fact that CORINE Land Cover is the only dataset containing the 'mixed forest' category, makes it outstandingly valuable. Such accuracy is undoubtedly related to the active participation of Slovak institutions in the development of this dataset. The dataset, however, does not contain any data for Ukraine, which is addressed in many initiatives focusing on the Carpathians bioregion. Therefore, a combination with other forest maps is needed.

The evaluation of datasets on tree species distribution did not yield as satisfactory results as datasets on forest and forest types. The spatial pattern of Silver fir distribution, according to both evaluated datasets (Brus et al. 2009; FORESTMOD 2013), was found to correspond with FMPs only very roughly, though the proposed modification using CORINE Land Cover brought substantial improvements (Figs 2 and 3). These facts may generate concern about the applicability of maps of other tree species with scattered distribution. Better results were obtained for species with contagious distribution – Norway spruce and European beech – in terms of both correlation analysis and visual match of maps with FMPs. However, the map ability to reproduce the total species areas in the country was poor, which may limit some applications for forest resources evaluation (e.g. carbon stocks). Hence, neither did the use of a number of national forest inventory data in both datasets allow for reaching a higher accuracy using methods based on the interpolation of point distributed data.

In pan-European evaluations, another problem may arise from the spatially varied accuracy, related to the variable density of source point data used for the interpolation of species proportions. Hence, a spatially explicit indicator of uncertainty, such as a map of kriging variance, should be used, along with species distribution maps. Generally, the evaluated species distribution maps should be used with care, and mainly for large-scale applications. In this regard, Tröltzsch et al. (2009) suggested that such maps can provide only a rough estimate of species distribution, and cannot replace highly detailed national inventory maps.

In addition to the datasets addressed in this study, there are, for example, products with global coverage, such as a global percentage tree cover map (DeFries et al. 2000), or the World Map of Forest Distribution (Ahlenius 2012), which were not considered because of their supposed limited informative value for Europe. However, exploring the quality of these data and their suitability for European conditions could be useful, and can be subjected to future research. The presented results indicated some deficiencies of evaluated datasets, and may initiate their future improvements. Owing to the overwhelming importance of European forest maps for the community and natural resource management such improvements are desperately needed.

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5.2 Future climate of the Carpathians: climate change hot-spots and implications for ecosystems.

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ORIGINAL ARTICLE

Future climate of the Carpathians: climate change hot-spots and implications for ecosystems

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Abstract The Carpathians are the largest European mountain range and harbour exceptional biodiversity. However, recent and anticipated changes in climate along with rapid social and economic development suggest that the region's values may not be sustained. We strived to identify the main regional climate change hot-spots and evaluate the distribution of climatically exposed land-use types and ecosystems. The analysis was based on 10 climate models driven by the emission scenario A1B. To identify the hot-spots, we adopted a methodology based on change trajectories in a multidimensional climate space. Three hot-spots were in the Western Carpathians (Czech Republic, Slovakia, and Hungary), two were in Ukraine, and three were in the Romanian and Serbian Carpathians. Regions with the highest aggregate climate exposure (i.e. above 70 % of the regional range) were mostly covered by broadleaved forests (39 %), agricultural land (30 %), and pastures and woodlands (15 %). These regions also contained 15 % of protected areas and 36 % of the total human population in the Carpathians. While growing season length was the main factor affecting hot-spot magnitude in the north-west, precipitation-related variables were the main factors in the east and south. Analysis of inter-climate model variability indicated that the level of confidence in hot-spot position and magnitude differed among hot-spots. In addition to identifying a large-scale regional pattern of climate change, we showed that there are sub-regions with remarkably high climate exposure. The hot-spot distribution in lower elevations suggests that Carpathian ecosystems in water-limited environment may be particularly exposed to climate change.

Keywords Climate exposure · Central and south-eastern Europe · Climate change adaptation · Drought · Biodiversity

Introduction

The Carpathian Mountains form the largest European mountain range and pass through Austria, Czech Republic, Slovakia, Poland, Hungary, Ukraine, Romania, and Serbia (Ruffini et al. 2006). Adjacent populated areas are functionally linked to the mountains and rely on a wide range of ecosystem services (Gurung et al. 2009; Grêt-Regamey

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et al. 2012). Countries with transitional economies cover a substantial part of the Carpathians, and overexploitation of natural resources and other indicators of unsustainable management are evident across the region (Schulze 2002; Knorn et al. 2012). Such practices may cause some ecosystems and human communities to be particularly sensitive to climate change. At the same time, the socio-economic capacity to adapt to anticipated threats is inadequate because of the relatively low performance of regional economies and the generally low level of public awareness regarding the need to adapt to climate change (Grothmann and Patt 2005; Fischer et al. 2005; Hlásny et al. 2014).

Recent observations indicate changes in the long-term quasi-equilibrium of diverse physical and biological systems in the Carpathians (Gurung et al. 2009; Spinoni et al. 2015). The frequency of extreme hydrological events has been increasing over the last decades and likely reflects recent changes in the climate (Easterling et al. 2000; Gurung et al. 2009). The Carpathians face accelerated vegetation dynamics with potentially adverse effects on biodiversity (Mihai et al. 2007; Martazinova et al. 2011; Solár and Janiga 2013), including the undesired influx of alien species (Simpson and Prots 2013). Recent observations indicate a substantial increase in the rate of forest disturbances including windthrows, forest fires, and pest outbreaks (Hlásny and Sitková 2010; Temperli et al. 2013) that adversely affect the provision of numerous ecosystem goods and services. Such disturbances also act as positive feedback to climate change through episodic releases of large amounts of carbon (e.g. Kurz et al. 2008; Seidl et al. 2014).

Information on the spatial variability of anticipated changes in climate is requested for vulnerability assessment and spatially targeted adaptation planning (Baettig et al. 2007; de Sherbinin 2014). The identification of climate change hot-spots based on the integration of diverse climate projections and other data has been increasingly used to assess the patterns and magnitude of climate exposure or vulnerability of various regions (e.g. Giorgi 2006; Baettig et al. 2007; Diffenbaugh et al. 2008; Ericksen et al. 2011; Diffenbaugh and Giorgi 2012; Piontek et al. 2014). The increasing resolution of climate modelling output, which can currently describe small-scale atmospheric processes and regionally important climate–orographic patterns (Farda et al. 2010), has resulted in the initiation of a number of regional studies, including specific research on regional climate change hot-spots (e.g. Midgley et al. 2011; Hagenlocher et al. 2014). Recent research has also provided comprehensive evaluation of climate models performance (Flato et al. 2013) as well as options for narrowing the uncertainty of climate projections (Hawkins and Sutton 2011), which might provide a useful support to climate change impact studies.

In this study, we provide new information on the magnitude, spatial trends, and variability of projected climate change in the Carpathians. So far, such information has been available mostly at a scale of countries extending into the Carpathians (e.g. Pongrácz et al. 2011, 2013; Bartholy et al. 2013; Micu et al. 2015), covering only a part of the region, or using a limited number of climate projections (Belda et al. 2015). Moreover, no hot-spot analyses have been conducted in the region. We adopt the methodology for global hot-spot identification that evaluates trajectories of change in a multidimensional climate space. We focus on climate exposure hot-spots (Giorgi 2006; Diffenbaugh and Giorgi 2012; Gu et al. 2014; Torres and Marengo 2014) rather than complex vulnerability hot-spots (Barnett et al. 2008; Piontek et al. 2014) or specific hot-spots related to human population migration (Samson et al. 2011) or other phenomena. We strive to identify the main land-use types and ecosystems of the Carpathians that are likely to experience high climate exposure in the future to encourage scientists and professionals to concentrate on these land-use types and ecosystems in climate change vulnerability assessment and adaptation planning. At the same time, we identify percentages of the human population in the Carpathians residing in climatically highly exposed regions; these human communities are likely to be directly affected by the declining provisioning of ecosystems goods and services as well as by the increasingly unfavourable climate. The importance of this research is underscored by numerous European or regional initiatives addressing the Carpathian region, including climate change vulnerability assessments, biodiversity and climate mapping, and adaptation (Turnock 2002; Gurung et al. 2009; Spinoni et al. 2015; Carpathian EcoRegion Initiative; Carpathian Convention; WWF Danube-Carpathian Programme, etc.).

Data and methods

Study region

This study used the Carpathian border designated by the Carpathian EcoRegion Initiative (CERI, http://www.carpates.org/) and the Carpathians Environment Outlook (KEO 2007) (Supplementary material A, Fig. A1). The region, which has an area of 229,966 km^2, contains the main Carpathian mountain range and adjacent foothills and lowlands; hence, the region includes a broad range of ecosystems and land uses. The current climate of the Carpathians (1961–1990), which was evaluated according to geomorphologic sub-provinces (Kondracki 1989), is described in Supplementary material A.

Climate data

Past climate data (1961–1990) used in this study are based on the daily data provided by the E-OBS database (Haylock et al. 2008) combined with the monthly CRU TS 1.2 (Mitchell et al. 2004) gridded data set. The future climate (2021–2050 and 2071–2100) was investigated based on 10 RCM–GCM (regional climate model–general circulation model) combinations provided by the ENSEMBLES FP6 project (van der Linden and Mitchell 2009). The models used were selected from the 32 models available in the ENSEMBLES database based on the following criteria: (1) spatial resolution of 25 × 25 km and (2) continuous coverage from 1951–2100 (for additional details, see Dobor et al. 2015). All climate projections were driven by the A1B greenhouse gas emission scenario (Nakicenovic and Swart 2000).

Because the direct use of RCM data is limited by systematic errors in the simulated variables (Christensen et al. 2008, Dosio and Paruolo 2011), data used in this study were bias-corrected following Dobor et al. (2015).

Given its regional scale, the current study requires high-resolution climate maps capturing the regional orographic pattern in the Carpathians. To produce such maps, we used kriging with external drift, a spatial interpolation method that was previously found suitable for the interpolation of climate data (Hudson and Wackernagel 1994). We used a digital elevation model with spatial resolution of 250 m (Jarvis et al. 2008) as a supportive variable correlated with all climate variables used in the current study. The climate maps were produced with the geostatistical software ISATIS (Geovariances, France).

Identification of climate change hot-spots

We modified the method proposed by Diffenbaugh and Giorgi (2012), which uses the standard Euclidean distance (SED) to quantify the aggregate climate change (ACC) in a multidimensional climate space between the present and future periods (Williams et al. 2007). The ACC is given as:

$$\mathrm{ACC} = \sqrt{\left(\sum_{i=1}^{n} \mathrm{SED}_v\right)}$$

where

$$\mathrm{SED}_v = (\Delta_v / max[\Delta_v])^2$$

Δ_v is the value of change in climate variable v at each grid point in the study area between two periods (1961–1990 and 2071–2100 in this study), and $max[\Delta_v]$ is a maximum value of change in variable v over the entire study area between the two periods.

We recalculated ACC to represent a percentage of the maximum permissible change, which is defined as the square root of the number of variables used for hot-spot identification (n):

$$\mathrm{ACC}_{\%} = \frac{\mathrm{ACC}}{\sqrt{n}} * 100$$

The identification of hot-spot positions is hampered by a large-scale north-west to south-east trend in the climate exposure of the Carpathians that causes the highest values of $\mathrm{ACC}_{\%}$ to occur in the south of the region. Hence, highly exposed locations with sub-regional importance (e.g. Western Carpathians) would not be identified. Therefore, we extracted a spatial trend from the $\mathrm{ACC}_{\%}$ surface and identified the hot-spots in positions where the residual $\mathrm{ACC}_{\%}$ (R-$\mathrm{ACC}_{\%}$) is above the 95 % quantile. Because the magnitude of the R-$\mathrm{ACC}_{\%}$ in hot-spots is more or less equal across the Carpathians, we used the original $\mathrm{ACC}_{\%}$ values (i.e. those containing trend) to evaluate hot-spot magnitude. The trend-containing data were also used to evaluate the relative contribution of the underlying climate variables to the $\mathrm{ACC}_{\%}$ for all hot-spots. Therefore, while hot-spot positions have sub-regional importance, their magnitude allows their comparison at a pan-Carpathian scale.

The variables used to calculate $\mathrm{ACC}_{\%}$ are precipitation totals during the growing season (April to September) (PTGS), growing season length (GSL), consecutive number of dry days (CDD), number of days with maximum air temperature exceeding 30 °C (T30), and the Ellenberg climate quotient (EQ) (for the justification of this selection, see Supplementary material B).

We calculated $\mathrm{ACC}_{\%}$ and R-$\mathrm{ACC}_{\%}$ for all 10 RCMs (Supplementary material G); R-$\mathrm{ACC}_{\%}$ based on the average climate projection was used for hot-spot identification. The uncertainty in hot-spot positions associated with inter-climate model differences was evaluated using the map of coefficient of variation (CV, ratio of standard deviation to mean climate projection in per cent). The CV was calculated for both $\mathrm{ACC}_{\%}$ and R-$\mathrm{ACC}_{\%}$.

Land-cover types, ecosystems, and population data

We used the Corine Land Cover data set (EEA 2006; CLC) to identify dominant land-cover categories in climatically highly exposed areas in the Carpathians (i.e. those areas with R-$\mathrm{ACC}_{\%} > 70$ % quantile, Supplementary material H). Because the data set was not available for Ukraine, we classified the Landsat satellite imagery and derived a map consistent with the CLC (Supplementary material D).

Forest tree species composition was taken from the results of statistical mapping of forest tree species in Europe (Brus et al. 2011) and from the Forest Management Plans of Slovakia (National Forest Centre, internal data). The natural vegetation of the Carpathians was evaluated based on a map developed by Bohn et al. (2004). The indicative information on non-forest vegetation was taken from several data sources such as the Carpathian Biodiversity Information System (CBIS, Carpathian EcoRegion Initiative) or Carpathian Integrated Biodiversity System (CCIBIS, WWF Danube-Carpathian Programme). The map of nature conservation areas in the Carpathians was produced based on a combination of national environmental databases and the maps of the Carpathian Network of Protected Areas (http://www.carpathianparks.org) and NATURA 2000 sites.

The population density grid of the European Union (Gallego 2010) was used to estimate the percentage of the human population living in highly exposed areas. Because this data set did not include Serbia and Ukraine, rougher data based on the local administrative units (LAU 1) were used instead (Ruffini et al. 2006).

Results

Spatial pattern of climate change

We present here future climate exposure of 14 geomorphologic units in the Carpathians based on 10 climate models for periods 2021–2050 and 2071–2100, compared to the period 1961–1990. The multi-model mean projection indicated an increase in the mean annual air temperature of 3.2–3.8 °C by the end of the century in the Carpathians, although some locations show an increase of up to 5.1 °C (details are given in the Supplementary material E).

While T30 in the Western and Eastern Carpathians was projected to increase by 18–30 days in the period 2071–2100, the projected increase in the Transylvanian Plateau, Serbian, and Western Romanian Carpathians was 33–48 days. The maximum change in T30, which was projected by HadRM3Q0–HadCM3Q0, was an increase of 65 days.

In the Western Carpathians, most models showed that PTGS in 2021–2050 would be more or less equal to PTGS in the reference period, but that PTGS would decrease by up to 10 % in 2071–2100. A mean decrease in precipitation of 15–27 % was projected for the rest of the Carpathians; however, the inter-model variability was high and ranged in the Serbian Carpathians, for example, from −7 to −47 %.

The pattern of change in CDD was mostly unclear, but an increase from the north-west to the south-east was apparent. While CDD was projected to decrease by about 4 days (from 17 to 13) in the Outer Western Carpathians, CDD was projected to increase from 18 to 21 days in the Serbian Carpathians. The pattern of change was unclear for the rest of the region, and inter-model variability was high.

EQ values in the reference period ranged from 10 to 85. Most of the Carpathians had values up to 30, but a small area in the Transylvanian Plateau had extreme values. Future projections indicated that the climate will become drier from the Western Carpathians (by 5 units) towards the Eastern and Serbian Carpathians (by 13 units). Locally, an increase in EQ values of up to 27 units occurred by the end of the century.

GSL was projected to increase across the Carpathians relatively uniformly by 10–20 days in 2021–2050 and by 30–40 days in 2071–2100; the inter-model variability, however, was high.

Climate change hot-spots

The magnitude of the original (i.e. not detrended) $ACC_{\%}$ increased from the north-west towards the south-east of the Carpathians. $ACC_{\%}$ in the Outer Western Carpathians was 51 to 53 % of the maximum permissible change in the Carpathians (all-model average $ACC_{\%}$ in CZ_{HS} and $SK\text{-}PL_{HS}$), while $ACC_{\%}$ in the Serbian Carpathian hot-spot (RS_{HS}) was 76 % (Table 1). $ACC_{\%}$ values were high in the main lowlands and intra-Carpathians valleys but lower on the main mountain crest. Inter-climate model variability of $ACC_{\%}$ was nearly equal in most of the Carpathians (the CV ranged from 8 to 13 %), except at RS_{HS}, where the CV was 17 % (Fig. 2a).

The extraction of a quadratic spatial trend from $ACC_{\%}$ generated normally distributed residuals suitable for hot-spot identification for all 10 climate models (Supplementary material G). The classification of the all-model average $R\text{-}ACC_{\%}$ using the threshold of 95 % quantile produced eight spots with remarkably high climate exposure, and these were located mostly in the Carpathian lowlands and foothills (Fig. 1). The CV was substantially higher for $R\text{-}ACC_{\%}$ than for the original trend-containing values (Fig. 2b); the 25 and 75 % quantiles of CV were 43 and 149 % for $R\text{-}ACC_{\%}$, and 9.4 and 13.6 % for $ACC_{\%}$. Four hot-spots ($SK\text{-}HU_{HS}$, $UA\text{–}North_{HS}$, $UA\text{–}South_{HS}$, and $RO\text{-}East_{HS}$) were in locations where the CV of $R\text{-}ACC_{\%}$ had relatively low values (22–56 %), while the remaining hot-spots were in locations with high inter-model variability (110–124 %).

In the Western Carpathians, two hot-spots (CZ_{HS} and $SK\text{-}PL_{HS}$) of almost equal magnitude, i.e. with $ACC_{\%}$ values near 50 %, were identified (Table 1). CZ_{HS} is located in the lowland of Moravia (Czech Republic), while $SK\text{-}PL_{HS}$ is adjacent to the mountain range of High Tatras

Table 1 Magnitude and inter-model variability of the aggregate climate change in hot-spots, magnitude and inter-model variability of change in underlying climate variables in hot-spots and relative contribution of five underlying climate variables to hot-spot magnitude

Code	Hotspot	$ACC_{\%}$		Climate variable									
				CDD		EQ		GSL		PTGS		T30	
		$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	REL	$\bar{x} \pm SD$	REL	$\bar{x} \pm SD$	REL	$\bar{x} \pm SD$	REL	$\bar{x} \pm SD$	REL
1	CZ_{HS}	53 (±4)	42–60	−3 (±3)	16	+6 (±6)	6	+40 (±7)	59	−3 (±16)	8	+23 (±9)	12
2	$SK\text{-}HU_{HS}$	59 (±5)	51–63	−2 (±4)	20	+10 (±8)	11	+34 (±6)	33	−13 (±13)	10	+37 (±11)	26
3	$SK\text{-}PL_{HS}$	51 (±7)	37–62	−5 (±2)	34	+5 (±4)	4	+36 (±10)	48	−8 (± 5)	9	+12 (±6)	4
4	$UA\text{–}North_{HS}$	60 (±7)	53–63	−7 (±2)	42	+6 (±6)	5	+36 (±8)	37	−12 (±15)	12	+16 (±9)	4
5	$UA\text{–}South_{HS}$	58 (±6)	53–61	−1 (±3)	6	+11 (±7)	15	+33 (±6)	33	−20 (±9)	19	+37 (±10)	26
6	$Trans_{HS}$	58 (±7)	48–66	−4 (±2)	24	+9 (±7)	9	+30 (±7)	27	−17 (±14)	15	+36 (±10)	25
7	$RO\text{-}East_{HS}$	72 (±7)	64–80	+1 (±4)	10	+19 (±11)	27	+30 (±8)	17	−27 (±14)	21	+46 (±10)	25
8	RS_{HS}	76 (±13)	71–80	+4 (±3)	12	+17 (±8)	25	+30 (±7)	15	−22 (±11)	18	+53 (±11)	30

$ACC_{\%}$ aggregate climate change in terms of the percentage of the maximum permissible change in the Carpathians, $\bar{x} \pm SD$ all-model average and inter-model standard deviation, *Range* inter-model range of $ACC_{\%}$ in hot-spot positions, *REL* relative importance of a climate variable with respect to $ACC_{\%}$ values in hot-spot positions (%), *CDD* cumulative dry days, *EQ* Ellenberg quotient, *GSL* growing season length, *PTGS* precipitation total during growing season; *T30* number of days with maximum daily air temperature exceeding 30 °C

Mts. at the Slovak–Polish border. At both hot-spots, GSL had the main effect on the $ACC_{\%}$, i.e. 59 % in CZ_{HS} and 48 % in $SK\text{-}PL_{HS}$ (Table 1). At $SK\text{-}PL_{HS}$, also CDD had substantial effect on $ACC_{\%}$ (34 %). The CV of $R\text{-}ACC_{\%}$ in both hot-spots was relatively high (110 and 124 %, respectively), suggesting uncertainty in these hot-spot positions.

The third hot-spot in the Western Carpathians ($SK\text{-}HU_{HS}$) is in the Pannonian Lowland at the border of Slovakia and Hungary. Its magnitude of 59 % was mainly affected by GSL (33 %), T30 (26 %), and CDD (20 %) (Table 1). CV of $R\text{-}ACC_{\%}$ of 56 % indicates relatively high agreement of climate models used.

Two hot-spots adjacent to the range of Carpathians are in Ukraine and reach 60 % ($UA\text{–}North_{HS}$) and 58 % ($UA\text{–}South_{HS}$) of the maximum permissible change. Among the eight hot-spots identified in this study, CDD had the largest influence at $UA\text{–}North_{HS}$ (42 %), followed by GSL (37 %). For $UA\text{–}South_{HS}$, the magnitude of $ACC_{\%}$ reflected the combined influence of GSL (33 %), T30 (26 %), PTGS (19 %), and EQ (15 %). The CV of $R\text{-}ACC_{\%}$ was relatively small in both hot-spots (31 and 53 %, respectively).

Two hot-spots were identified in Romania: one in the Transylvanian Plateau ($Trans_{HS}$) with a magnitude of 58 % and one in the Outer Eastern Carpathians ($RO\text{-}East_{HS}$) with a magnitude of 72 %. $Trans_{HS}$ reflected the combined influence of GSL (27 %), T30 (25 %), CDD (24 %), and PTGS (15 %). $RO\text{-}East_{HS}$ was influenced by EQ (27 %), T30 (25 %), PTGS (21 %), and GSL (17 %). The main difference between the Romanian hot-spots was that while $Trans_{HS}$ was significantly affected by CDD (24 %), this variable had little effect in $RO\text{-}East_{HS}$. Although the CV of $R\text{-}ACC_{\%}$ was small in $RO\text{-}East_{HS}$ (22 %), the CV in $Trans_{HS}$ was high (109 %), suggesting uncertainty in the identification of the latter hot-spot.

The Serbian Carpathian hot-spot (RS_{HS}) had the highest $ACC_{\%}$ (76 %) and was affected by T30 (30 %), EQ (25 %), and PTGS (18 %), followed by GSL (15 %) and CDD (12 %). CV of $R\text{-}ACC_{\%}$ was large (108 %).

Land cover, ecosystems, and population distribution

The areas with high climate exposure, which are those with the $R\text{-}ACC_{\%} > 70$ % (Supplementary material H), are mostly covered by broadleaved forests (39 %), agriculture land (30 %) and pastures and woodlands (15 %) (Supplementary material I).

The exposed forests contain diverse species of oak (*Quercus* spp.), European beech (*Fagus sylvatica* L.), pines (*Pinus* spp.), and hornbeam (*Carpinus betulus* L.), plus other less important species. The natural vegetation in exposed regions is dominated by pre-Carpathian beech forests, Carpathian fir-beech and spruce-fir-beech forests,

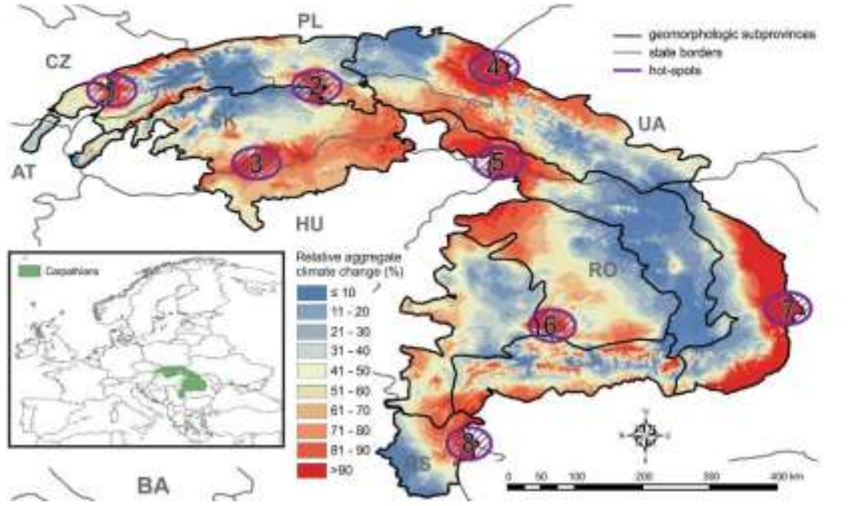

Fig. 1 Aggregate climate change in the Carpathians and climate change hot-spots (indicated by *numbers*) identified based on multi-model mean projection. Hot-spot codes are explained in Table 1

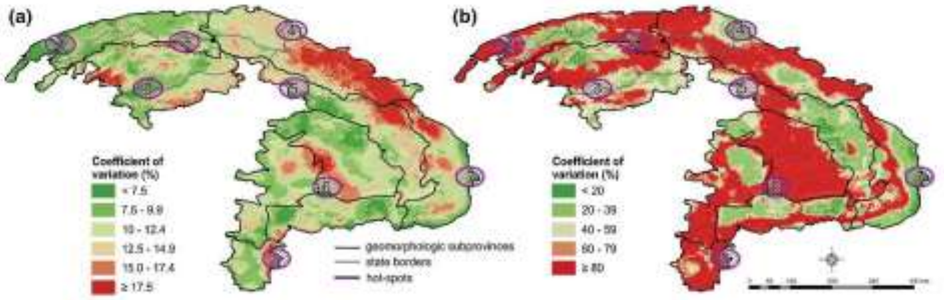

Fig. 2 Coefficient of variation of the aggregate climate change (**a**) and of the residual aggregate climate change (**b**). The coefficient indicates the degree of uncertainty related to differences in the 10 climate models used for the analysis. Also indicated are the positions of eight climate change hot-spots identified based on the mean climate projection

Pannonian-pre-Carpathian sessile oak-bitter oak forests, and Pannonian-pre-Carpathian hardwood alluvial forests (Bohn et al. 2004). Some vegetation types of the Carpathians occur exclusively in the exposed regions (Supplementary material J).

The exposed regions comprise a variety of primary and secondary thermo- and xerophilous communities of the class *Festuco-Brometea* Br.-Bl. et Tüxen ex Soó 1947, and communities of the secondary mesic and wet meadows and pastures on nutrient-rich soils of the class *Molinio-Arrhenatheretea* Tüxen 1937. The meadow vegetation contains mainly the mesic meadows of lower altitudes (alliance *Arrhenatherion elatioris* Luquet 1926) and manured pastures of lower altitudes (alliance *Cynosurion cristati* Tüxen 1947 nom. cons. propos.) (Janišová et al. 2007). Most of the grasslands have been traditionally grazed, but some types in more productive habitats have also been mown (Chytrý 2007).

Of the total area of nature conservation areas (i.e. national parks, protected landscape areas, and nature reserves) in the Carpathians, 23 % is distributed in the exposed regions (Supplementary material K). Parts of the most important Carpathian nature conservation areas, such as the Bükki National Park and the Duna-Ipoly National Park in Hungary, and the Djerdap National Park on the border of Romania and Serbia, lie in the exposed regions. Twenty-three percentage of the NATURA 2000 sites (under both bird and habitat directive) is in the exposed regions as well, with the highest share in the Outer Eastern Carpathians North (47 % of NATURA sites in the geomorphologic unit).

Approximately 36 % of the total human population in the Carpathians live in the exposed regions (Supplementary material K).

Discussion

In this study, we have explored how climate in the Carpathians is likely to develop in the future and whether the spatial pattern of "aggregate climate change" includes regions that are particularly exposed to climate change and should be chiefly considered in complex vulnerability assessment and adaptation planning. This study adds to the recent research efforts addressing the regional patterns of climate exposure or of complex vulnerability (e.g. Midgley et al. 2011; Gu et al. 2014; Hagenlocher et al. 2014), which are meant to support the targeted allocation of resources for climate change adaptation. Indeed, the drawbacks and deficiencies in these assessments, which concern both the analytical aspects of hot-spot identification (Freudenberg 2003; Diffenbaugh and Giorgi 2012) and the use of hot-spots in decision- and policy-making (Barnett et al. 2008; de Sherbinin 2014), have been repeatedly stressed.

Methodological aspects

The application of global hot-spot mapping methodology based on the studies of Giorgi (2006), Williams et al. (2007), and Diffenbaugh and Giorgi (2012) at a regional scale raises several questions concerning the proper interpretation of the regional hot-spot patterns. That the maximum change in the underlying climate variables used for the $ACC_{\%}$ calculation was identified in the Carpathians rather than on the global scale obviously indicates that the identified hot-spot patterns are strictly specific to the Carpathian region. For this reason, for example national assessments should avoid interpreting the identified hot-spots as hot-spots of national importance. Assessing the maximum change parameters within the Carpathian territory also suggests that values of $ACC_{\%}$ higher than those in the hot-spots (i.e. above 100 %) may be distributed in areas surrounding the investigated region or elsewhere; for example, $ACC_{\%}$ values above 100 % occur south of the Carpathians in Hungary and Romania, suggesting that these areas are likely to experience higher climate exposure than the Carpathians themselves.

The use of spatially detrended $ACC_{\%}$ for hot-spot identification represents a substantial modification of the original procedure. Such a modification was necessary to be applied to cope with the presence of the north-west to south-east gradient in the projected climate exposure that was present in all climate variables used for $ACC_{\%}$ calculation, and consequently, in the $ACC_{\%}$ itself. Trend extraction from the original $ACC_{\%}$ values allowed us to identify the hot-spots by setting a unique threshold in the R-$ACC_{\%}$ (i.e. the 95 % quantile) for the entire Carpathians and prevented hot-spot accumulation in the south of the Carpathians, as would be the case with the original trend-containing $ACC_{\%}$. The latter pattern would provide information of questionable value for most of the region. It follows that hot-spots identified using the R-$ACC_{\%}$ should be thought of as having sub-regional rather that pan-Carpathian relevance; however, such a sub-regional scale can be more useful for regional vulnerability assessment and adaptation planning. Regardless, we also preserved the information on the $ACC_{\%}$ magnitude in hot-spot positions based on the original trend-containing data, which can be valuable for specific pan-Carpathian evaluations.

Unlike our study, most other studies have identified hot-spots based on the visual evaluation of some type of the aggregate climate change map or other indicator (e.g. Giorgi 2006; Baettig et al. 2007; Gu et al. 2014). For example, Giorgi (2006) argues against the importance of setting a unique threshold that would allow for hot-spot identification, because hot-spot analysis primarily compares regions with each other and does not provide an absolute measure of change. We argue that an approach based on classification of a residual map, as was done in the current study, is more rigorous than one based on visual investigation and that the classification of a residual map can be particularly useful when large-scale trends might obscure regionally important hot-spot patterns. In most cases, however, both approaches are likely to produce similar results.

The selection of climate variables used for $ACC_{\%}$ calculation was based on expert decision and was justified based on the importance of the selected variables for regional ecosystem dynamics (Supplementary material B). For example, Diffenbaugh and Giorgi (2012) and Gu et al. (2014) used seven climate variables for each of four seasons, yielding a 28-dimensional climate space; Giorgi (2006) and Torres and Marengo (2014) used four variables for two seasons to calculate a Regional Climate Change Index (RCCI); and Baettig et al. (2007) used nine combinations of climate elements and seasons to calculate a Climate Change Index (CCI). We argue that such analyses were likely to be affected by an inter-variable correlation (for example, when the same variable is evaluated for several seasons), which could result in the overestimation of the effects of some variables. Therefore, we suggest that some degree of control of inter-variable correlation, as performed in the current study, should be applied.

The inter-model range of the underlying climate variables was high (Supplementary material F), even though the used models were driven by only a single emission scenario. The latter fact raises the question as to whether the used ensemble of climate models represents an adequate portion of the uncertainty in future climate development. In this regard, Hawkins and Sutton (2011) suggested that uncertainty in precipitation related to the difference in emission scenarios is relatively small by the end of the twenty-first century in Europe, while uncertainty in precipitation related to the difference in climate models driven by the same radiative forcing is substantial. However, this is not the case for temperature. On this basis, we argue that the ensemble of climate change scenarios used in our study contained a substantial part of the uncertainty related to future climate development, although temperature-related uncertainty was probably underestimated. Moreover, a quality-controlled and bias-corrected climate data set driven by an emission scenario other than that used in the current study (Dobor et al. 2015) is not currently available for the region.

As our investigation used present-day data on ecosystems, land use, nature conservation, and human population distribution, one may question whether it is appropriate to evaluate future climate exposure for these present-day systems. Moreover, numerous studies have provided scenarios on how ecosystems, land use, and human population distributions are likely to develop in the future (e.g. Rounsevell et al. 2006), and these kinds of information could also be used in the investigated region. We argue, however, that the concurrent use of a number of scenario-based modelling outputs (i.e. outputs for climate, ecosystems, and human populations) would likely generate uncertain information with limited applicability. Therefore, we opted to assume a baseline scenario, which can inform vulnerability assessment studies about the type of climate exposure of ecosystems and other features provided no changes in their distribution occur. In fact, sensitivity and adaptive capacity variables used in vulnerability studies often represent current rather that future state, which needs to be considered in the interpretation of such studies (Preston et al. 2011; de Sherbinin 2014).

Ecological and environmental inferences

The identified hot-spots are mainly located in lowland and foothill areas adjacent to the main mountain range of the Carpathians. At the same time, the magnitude of the aggregate change (in terms of the trend-containing $ACC_{\%}$) increased towards the south; the magnitude of $ACC_{\%}$ was ca. 25 % higher for the Romanian–Serbian hot-spot (RS_{HS}) than for the CZ_{HS} and PL_{HS} located in the Western Carpathians (76 vs. 51–53 % of the maximum permissible change). Such findings indicate that the areas that are most likely to experience excessive climate exposure are those that currently contain semi-arid ecosystems (forest steppe or open woodland), which act as important barriers to landscape aridification (Sun and Liu 2013), the climate-sensitive lower distributional limit of closed forests (Mátyás 2010; Mátyás and Sun 2014), as well as commercially and ecologically valuable broadleaved forests in the foothills of the main mountain crest. Interestingly, Mátyás (2010) suggested that the climate vulnerability of such ecosystems has been largely unexplored until very recently as compared with, for example, mountain ecosystems.

Stagl et al. (2015) suggested that information on climate exposure might be critical for climate-influenced decision-making in protected areas. That 23 % of the Carpathians' nature conservation areas lie in climatically exposed regions generates concern about the effects of climate change on the regional biodiversity (Turnock 2002). Such effects are generally expected to be adverse (Thuiller et al. 2005, 2007; Bellard et al. 2012), what is particularly relevant for Carpathians, which represent a unique reservoir of many endemic plant and animal species of the European importance (Grodzińska et al. 2004; Kuemmerle et al. 2010). Differences in climate sensitivity among the main ecosystem types in the Carpathians may result in differences in the responses of biodiversity to climate change. For example, climate change might induce habitat destruction in Carpathian forests that are located near their xeric distributional limit and that have high climate sensitivity (Lakatos and Molnár 2009; Mátyás et al. 2010; Hlásny et al. 2014). On the other hand, Carpathian grasslands, 24 % of which are distributed in the highly exposed areas, can be resilient to drought in the face of climate change and can help maintain ecosystem functioning even under increasing climate exposure (Craine et al. 2012).

Our assessment showed that the Carpathians include extensive, mostly mountainous areas with lower $ACC_{\%}$ values than the rest of the region. This finding might seem surprising because some studies have suggested that the warming rate is greater at mountains than at lower elevations (e.g. Pepin et al. 2015). The evidence for this difference in warming rate has been questioned, however, based on methodological and other concerns (e.g. Rangwala and Miller 2012). Moreover, the aggregate climate exposure evaluated in this study was based on some climate variables that show geographic and topographic patterns different from that of the air temperature; hence, the specific pattern of $ACC_{\%}$ was found in our research.

The identified high climate exposure of Carpathian lowlands and foothills should not be misinterpreted to mean that the mountain areas have a low vulnerability to climate change. The vulnerability of mountain ecosystems to climate change is generally high (Briner et al. 2013), mainly because of the high climate sensitivity of these ecosystems resulting from, for example, the limited options for species to migrate (Jump et al. 2009). Our research, however, indicates that lowland and foothill Carpathian ecosystems are likely to experience substantial climate exposure. That the climate sensitivity of these ecosystems has not been well studied (Mátyás 2010) might generate concerns about our capacity to understand region's vulnerabilities and to take appropriate actions. Therefore, we suggest that future research should focus on the climate-related vegetation dynamics in climatically exposed semi-arid regions, which represent large areas in the Carpathian region, and such research might be critical for effective adaptation.

Finally, we determined that 36 % of the human population of the Carpathians resides in the exposed regions, a finding that highlights the importance of potential declines in ecosystem services such as air and water quality maintenance, or climate regulation (Patz et al. 2005; McMicheal et al. 2006) as well as of a direct effect of increasingly unfavourable climate on humans.

Socio-economic and management perspectives

Five of the eight hot-spots identified in this study are distributed in the Ukrainian, Romanian, and Serbian part of the Carpathians, where social and economic indicators are much lower than in the Western Carpathian countries (Czech Republic, Slovakia, Poland, and Hungary); moreover, the magnitude of ACC% was as much as 25 % higher in the former than in the latter region. The gross domestic product per capita in the period 2009–2011 in the Ukraine, Romania, and Serbia was only 35.8 % of that in the Western Carpathian countries (http://data.worldbank.org), which indicates a much lower adaptive capacity in the Ukraine, Romania, and Serbia. The low adaptive capacity of countries with transitional economies along with the high climate exposure of the south-eastern region of the Carpathians underscores the urgent need for increasing our understanding of this region's vulnerability and for exploring options for adaptation.

Although identification of climatically exposed regions and vulnerable social, physical, or biological systems helps set priorities for research and resource management, there is little evidence that hot-spot maps developed for various regions and sectors have influenced investment, research, or adaptation (de Sherbinin 2014). Despite the promotion of knowledge-based and data-driven decision-making (e.g. Vacik et al. 2013; Marušák and Kašpar 2015), there are factors in the region that hamper the use of vulnerability assessments in resource management. For example, none of the Carpathian countries has effective legislation regarding climate change adaptation, except for non-binding strategies (Merganičová et al. 2013), and this lack of legislation significantly reduces the transfer of knowledge gained from research to decision-making. The international scope of our study and of the identified hot-spots makes the transfer of knowledge even more difficult. In this regard, de Sherbinin (2014) suggested that national decision-makers often tend to distrust regional or international assessments because such decision-makers lack confidence in data not obtained under the supervision of national agencies. Indeed, there are reasons to question the quality of global or regional data, including those used in the current study (e.g. Trombik and Hlásny 2013), as well as relevance of inferences based on such data for decision-making at the national level. Still, researchers have repeatedly emphasized that natural resource management and conservation should be coordinated at a scale of bioregions (Turnock 2002; Chester 2006). Obviously, management at a regional scale (across the Carpathians, for example) will require global or regional assessment such as that presented in the current study.

Conclusions

Our study confirmed that the investigation of spatial variability of climate projections can help identify sub-regions that are particularly exposed to climate change. Using a novel methodology proposed in this study, we found out that, in addition to a large-scale north-to-south trend of climate warming and drying in the Carpathians, there are sub-regions with remarkably high climate exposure. Such highly exposed sub-regions were distributed mainly in the lowland to foothill areas, which suggests that Carpathian ecosystems located in water-limited environment can be particularly exposed to climate change. Hence, understanding drought effects and improving water-friendly landscape management may be central to adapting to climate change in extensive parts of the Carpathian region. These facts can help to set future research priorities and decide upon adaptation actions. Unfortunately, the dynamics of semi-arid ecosystems and their responses to climate change in the study region are insufficiently understood to enable effective adaptation.

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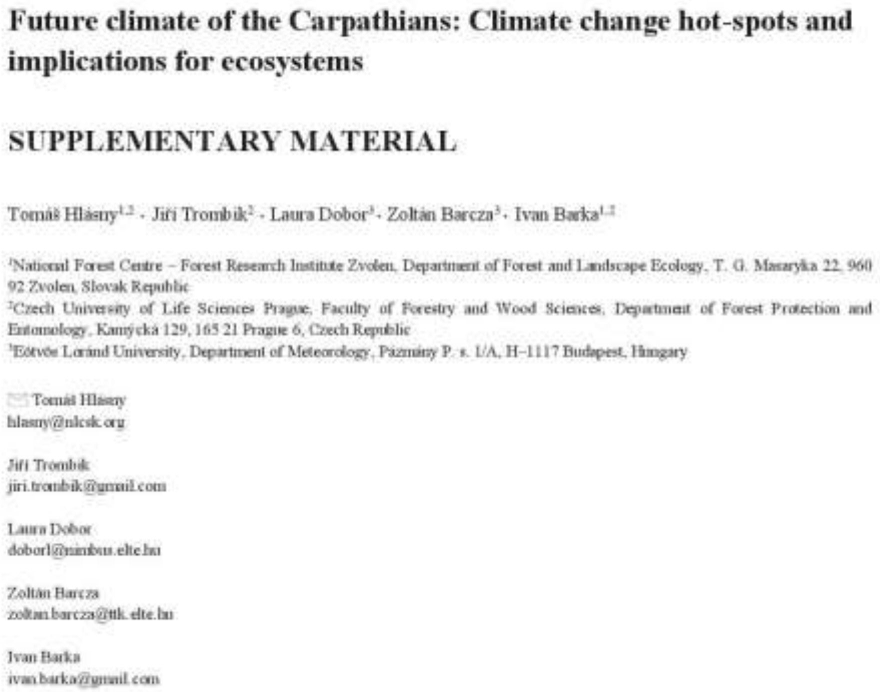

Future climate of the Carpathians: Climate change hot-spots and implications for ecosystems

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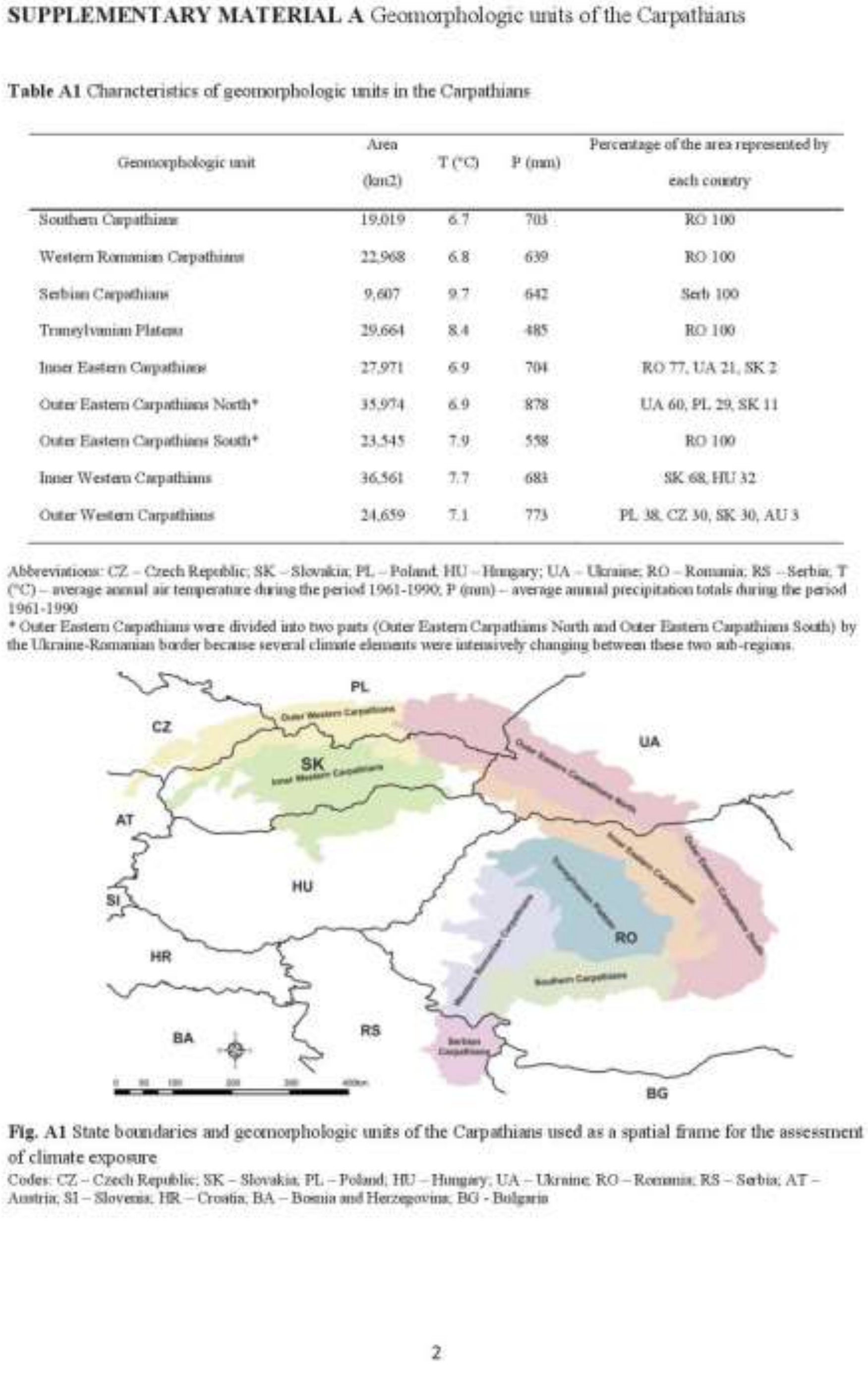


SUPPLEMENTARY MATERIAL A Geomorphologic units of the Carpathians

Table A1 Characteristics of geomorphologic units in the Carpathians

Geomorphologic unit	Area (km2)	T (°C)	P (mm)	Percentage of the area represented by each country
Southern Carpathians	19,019	6.7	703	RO 100
Western Romanian Carpathians	22,968	6.8	639	RO 100
Serbian Carpathians	9,607	9.7	642	Serb 100
Transylvanian Plateau	29,664	8.4	485	RO 100
Inner Eastern Carpathians	27,971	6.9	704	RO 77, UA 21, SK 2
Outer Eastern Carpathians North*	35,974	6.9	878	UA 60, PL 29, SK 11
Outer Eastern Carpathians South*	23,545	7.9	558	RO 100
Inner Western Carpathians	36,561	7.7	683	SK 68, HU 32
Outer Western Carpathians	24,659	7.1	773	PL 38, CZ 30, SK 30, AU 3

Abbreviations: CZ – Czech Republic; SK – Slovakia; PL – Poland; HU – Hungary; UA – Ukraine; RO – Romania; RS – Serbia; T (°C) – average annual air temperature during the period 1961-1990; P (mm) – average annual precipitation totals during the period 1961-1990

* Outer Eastern Carpathians were divided into two parts (Outer Eastern Carpathians North and Outer Eastern Carpathians South) by the Ukraine-Romanian border because several climate elements were intensively changing between these two sub-regions.

Fig. A1 State boundaries and geomorphologic units of the Carpathians used as a spatial frame for the assessment of climate exposure

Codes: CZ – Czech Republic; SK – Slovakia; PL – Poland; HU – Hungary; UA – Ukraine; RO – Romania; RS – Serbia; AT – Austria; SI – Slovenia; HR – Croatia; BA – Bosnia and Herzegovina; BG - Bulgaria

SUPPLEMENTARY MATERIAL B Definition of variables used for identification of climate change hot-spots and justification of their selection

The variables used to identify climate change hot-spots were selected from a broader set of variables based on two criteria: the relevance of a given variable as a driver of regional ecosystem dynamics, and inter-variable correlation < 0.8 of the Pearson's R (Table B1). The latter criterion was used to avoid redundancy in the data. In addition to considering the correlation of variable values, we also considered the correlation of differences in variable values between the future and reference climate because these differences were used to calculate aggregate climate change (Table B2).

- **Precipitation total during growing season (April-September) (PTGS)** is generally recognized as a key factor affecting the vigour, productivity, and distribution of vegetation including agriculture crops (Frank 2007; Al-Kaisi et al. 2013). At the same time, PTGS is broadly used as a predictor variable in species distribution mapping and in other predictive modelling (e.g., Garzón et al. 2007).
- **Consecutive dry days (CDD)** describes the average duration of rainless periods during the investigated 30-year periods (1961-1990 and 1971-2100). Dry days were defined as those with < 3 mm of precipitation because, given interception and evaporation losses, 3 mm of precipitation is unlikely to affect the physiological performance of vegetation (van de Salm et al. 2007); indeed differences between vegetation types and environments exist.
- **Number of days with maximum air temperature exceeding 30°C (T30)** is used as an indicator of extreme air temperatures. High temperatures are likely to reduce the physiological performance of diverse vegetation groups and can even increase mortality rates (e.g., Allen 2000; Bréda et al. 2006; Kipp et al. 2008; Hlásny et al. 2014). The combined effects of drought and high temperature are especially damaging (Rouault at al. 2006; Mátyás et al. 2010).
- **Ellenberg climate quotient (EQ)** is defined as the ratio of mean air temperature of the warmest month (MTWM) and the annual precipitation sum (AP): EQ = MTWM / AP × 1000. The quotient is a powerful predictor of the vigour and distribution of some forest tree species in Europe (Jensen et al. 2004; Fang and Lechovitz 2006; Czúcz 2011).
- **Growing season length (GSL)** is defined as the number of days per year with daily mean air temperature above 5°C. In the calculation of GSL, the growing season begins in spring with the first continuous sequence of 6 days above 5°C and ends in autumn with the first continuous sequence of 6 days below 5°C. GSL increases in response to climate change and can increase plant growth and productivity, mainly at higher elevations and latitudes, where GSL can be limiting factor (Grace et al. 2002, Reyes-Fox et al. 2014).

According to the inter-variable correlation matrix for the original variables (i.e., not for differences between the two periods), the correlation coefficients between GSL and T30 and between PTGS and EQ were 0.8; for the remaining variables, the coefficients ranged from -0.69 to 0.78 (Table B1).

The correlation of differences between the periods 2071-2100 and 1961-1990 can be thought of as a relevant indicator of redundancy in the data because the differences (or the percentage change in the case of PTGS) were used to calculate the aggregate climate change. Based on these differences, the correlation between EQ and PTGS, between T30 and PTGS, and between T30 and EQ reached or nearly reached the arbitrarily set threshold of 0.8 (Table B2). The correlation coefficients for the remaining pairs ranged from -0.31 to -0.79. This indicates that the selected variables were not so strongly correlated to justify their exclusion from the analysis.

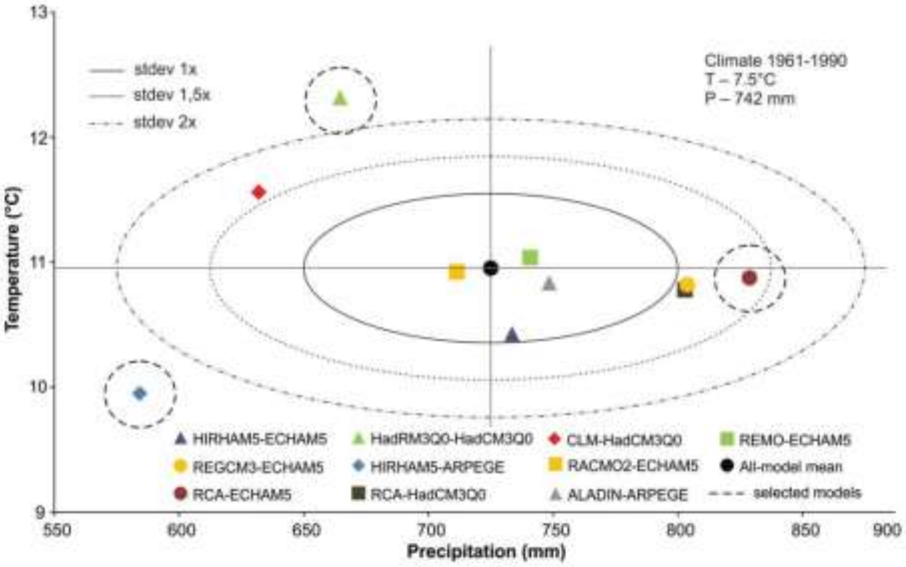
Table B1 Matrix of Pearson correlation coefficients for the original climate variables (i.e. not the differences) for the periods 2071-2100 and 1961-1990 that were used to identify climate change hot-spots

	PTGS	CDD	EQ	T30	GSL
PTGS	1.00	—	—	—	—
CDD	-0.70	1.00	—	—	—
EQ	-0.80	0.62	1.00	—	—
T30	-0.79	0.65	0.80	1.00	—
GSL	0.53	-0.31	-0.61	-0.63	1.00

Table B2 Matrix of Pearson correlation coefficients for the climate variables for the periods 2071-2100 and 1961-1990 that were used to identify climate change hot-spots. Correlations of differences between the two periods are indicated

	PTGS	CDD	EQ	T30	GSL
PTGS	1.00	—	—	—	—
CDD	-0.69	1.00	—	—	—
EQ	-0.80	0.70	1.00	—	—
T30	-0.71	0.76	0.78	1.00	—
GSL	-0.64	0.73	0.59	0.80	1.00

SUPPLEMENTARY MATERIAL C Temperature-precipitation chart used to characterize the 10 climate models used in the current study based on climate data for the period 2071-2100



In this diagram, the X-axis represents the precipitation totals during a growing season (IV-IX), and the Y-axis represents mean annual air temperature. The temperature-precipitation space is divided by the all-model mean values into four quadrants, in which the individual models are distributed. Three most contrasting models – HIRHAM-ARPEGE (cold-dry model), HadRM3Q0-HadCM3Q0 (hot-dry model), and RCA-ECHAM5 (temperature neutral-moist model) – are highlighted. Respective aggregate climate change maps are presented in the Supplementary material G.

SUPPLEMENTARY MATERIAL D Land cover of the Ukrainian part of the Carpathians based on the supervised classification of the Landsat satellite imagery

A supervised classification based on the Maximum Likelihood Classifier was used to classify the Landsat satellite imagery and to produce the map of the Ukrainian land cover; this map used categories identical to those of the Corine Land Cover data set (CLC). Spectral signatures of classified land cover categories were derived from the spectral reflectance data from the Landsat imagery within the CLC categories in the regions adjacent to Ukraine in Slovakia, Poland, and Romania, where CLC data are available. Moreover, a digital elevation model (based on EU-DEM and SRTM) was used to enhance the signatures by considering the altitudinal arrangement of land cover types. Google Maps was used to define the boundaries of training sites in greater detail. The Landsat TM scenes taken during the vegetation period in years 2007-2009 were used (granules 184-026, 184-027, 185-026, 185-027, 186-026, and 186-027).

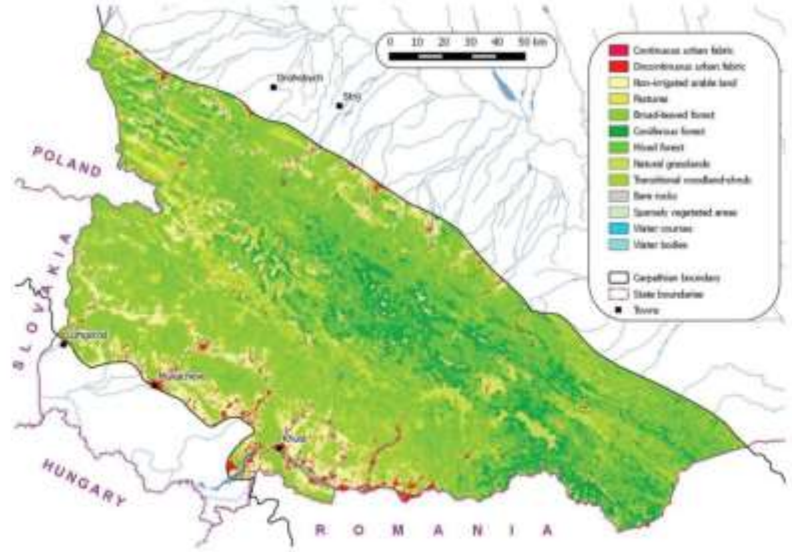


Fig. D1 Map of the land cover in the Ukrainian part of the Carpathians based on the supervised classification of the Landsat satellite imagery

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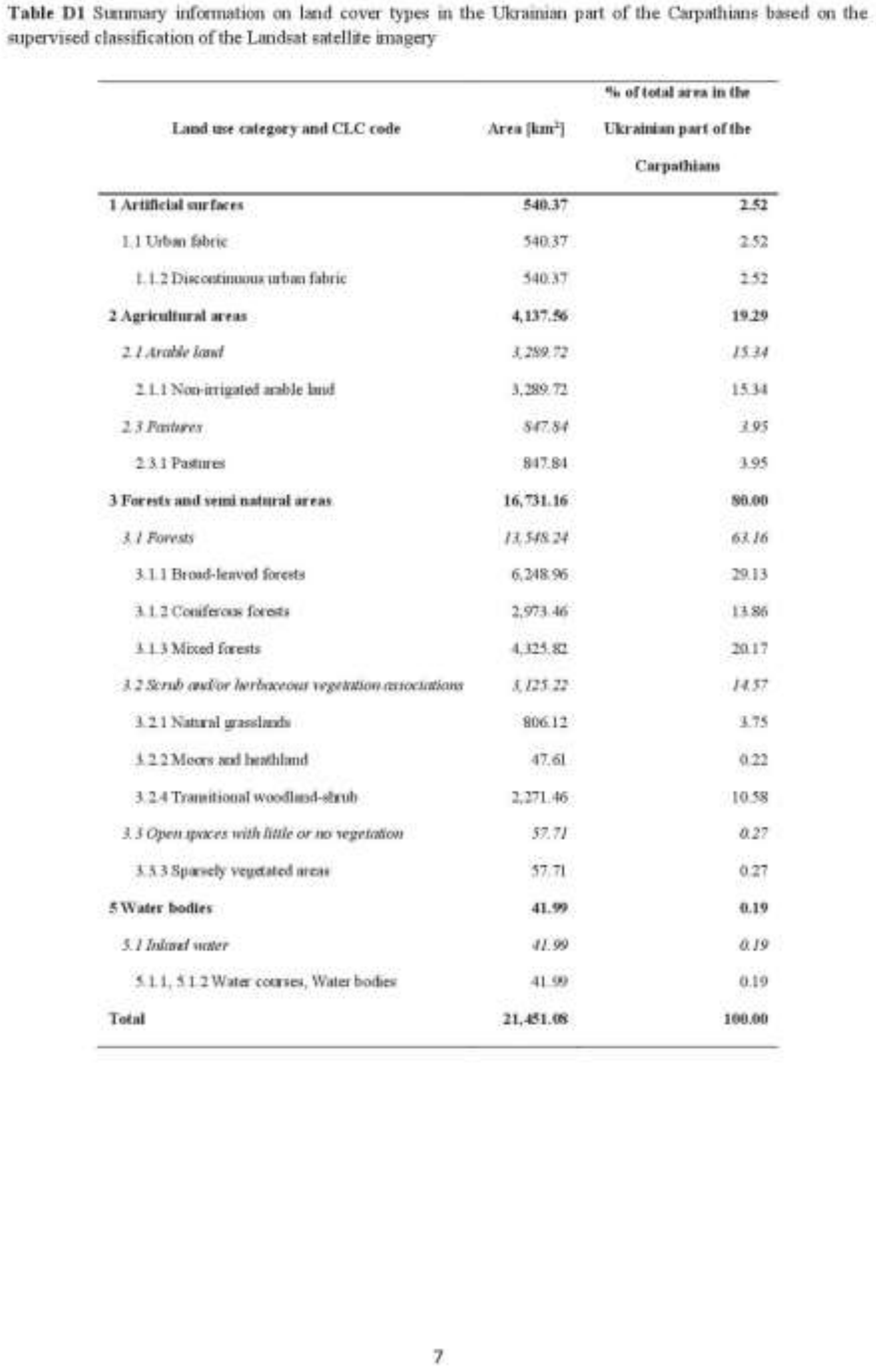


Table D1 Summary information on land cover types in the Ukrainian part of the Carpathians based on the supervised classification of the Landsat satellite imagery

Land use category and CLC code	**Area [km^2]**	**% of total area in the Ukrainian part of the Carpathians**
1 Artificial surfaces	**540.37**	**2.52**
1.1 Urban fabric	540.37	2.52
1.1.2 Discontinuous urban fabric	540.37	2.52
2 Agricultural areas	**4,137.56**	**19.29**
2.1 Arable land	*3,289.72*	*15.34*
2.1.1 Non-irrigated arable land	3,289.72	15.34
2.3 Pastures	*847.84*	*3.95*
2.3.1 Pastures	847.84	3.95
3 Forests and semi natural areas	**16,731.16**	**80.00**
3.1 Forests	*13,548.24*	*63.16*
3.1.1 Broad-leaved forests	6,248.96	29.13
3.1.2 Coniferous forests	2,973.46	13.86
3.1.3 Mixed forests	4,325.82	20.17
3.2 Scrub and/or herbaceous vegetation associations	*3,125.22*	*14.57*
3.2.1 Natural grasslands	806.12	3.75
3.2.2 Moors and heathland	47.61	0.22
3.2.4 Transitional woodland-shrub	2,271.46	10.58
3.3 Open spaces with little or no vegetation	*57.71*	*0.27*
3.3.3 Sparsely vegetated areas	57.71	0.27
5 Water bodies	**41.99**	**0.19**
5.1 Inland water	*41.99*	*0.19*
5.1.1, 5.1.2 Water courses, Water bodies	41.99	0.19
Total	**21,451.08**	**100.00**

SUPPLEMENTARY MATERIAL E Projected change of climate variables used for hot-spot identification with respect to geomorphologic units of the Carpathians

Numbers on the X-axes denote three periods: 1 – 1961-1990, 2 – 2021-2050, 3 – 2071-2100. The Y-axes indicate changes in variable values relative to the reference period (1961-1990); the value for the reference period is indicated in each panel. For precipitation totals during the growing season, the values are the percentages of change.

Black circle – all-model mean; Grey circles – 10 climate models; Vertical lines – standard deviations.

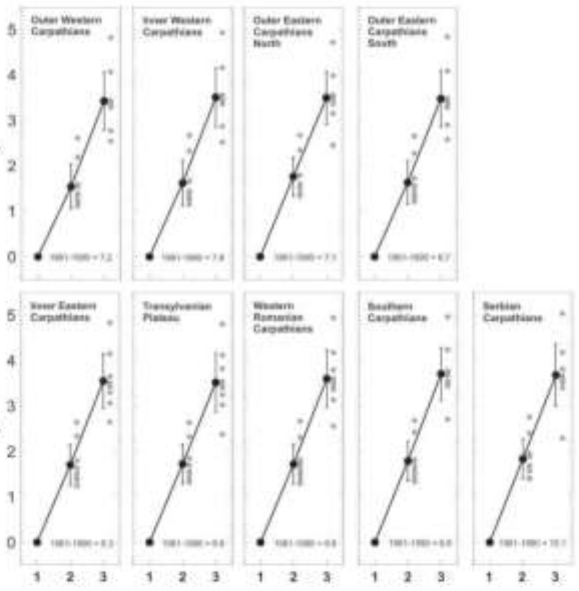


Fig. E1 Projection of mean annual air temperature based on 10 climate models

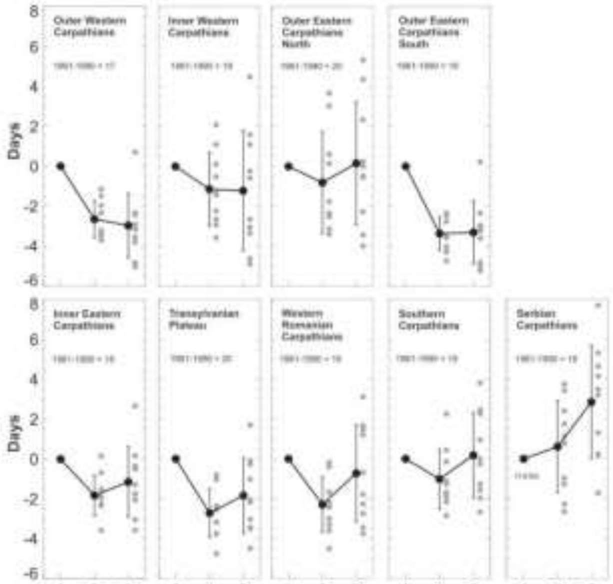


Fig. E2 Projection of the number of cumulative dry days based on 10 climate models

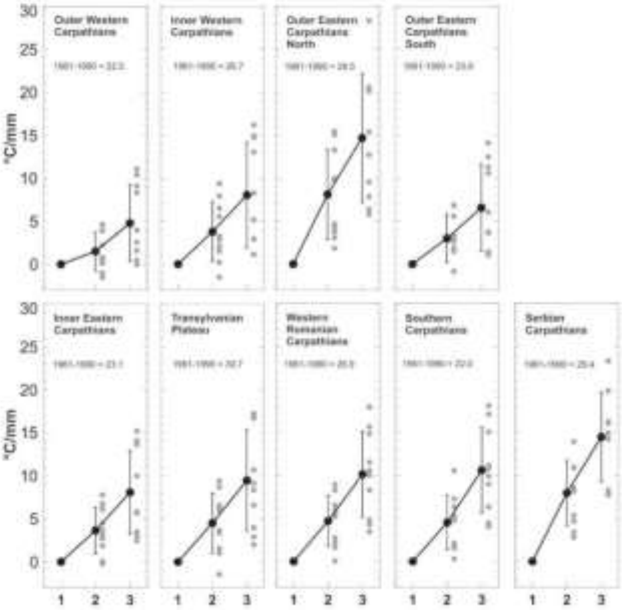


Fig. E3 Projection of Ellenberg climatic quotient based on 10 climate models

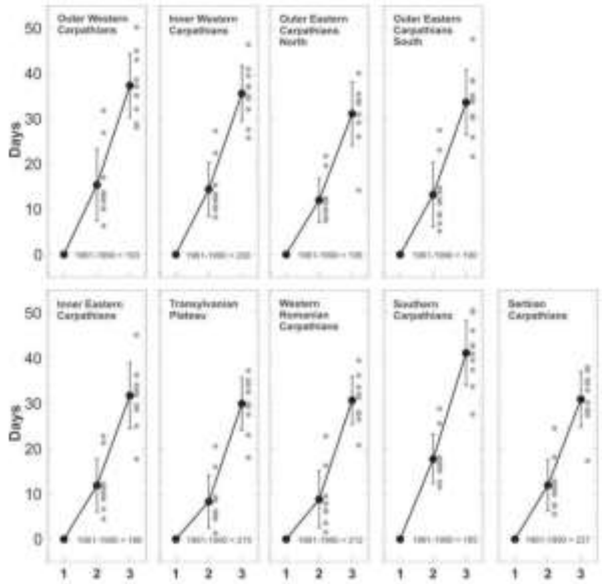


Fig. E4 Projection of growing season length based on 10 climate models

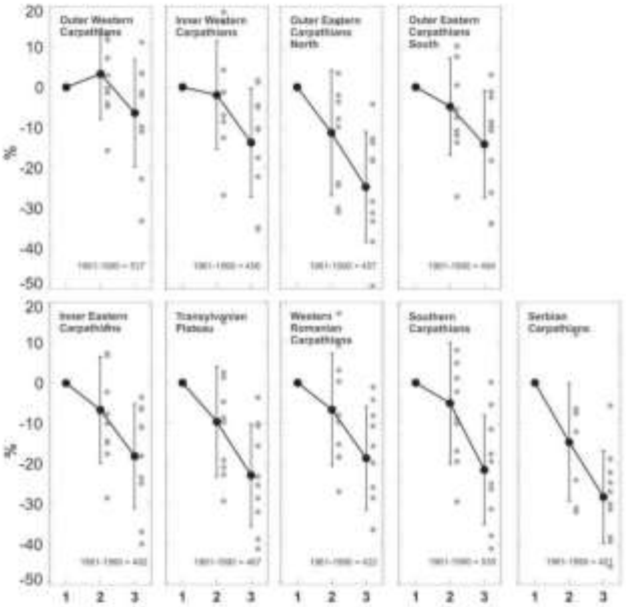


Fig. E5 Projection of precipitation totals during the growing season (April-September) based on 10 climate models

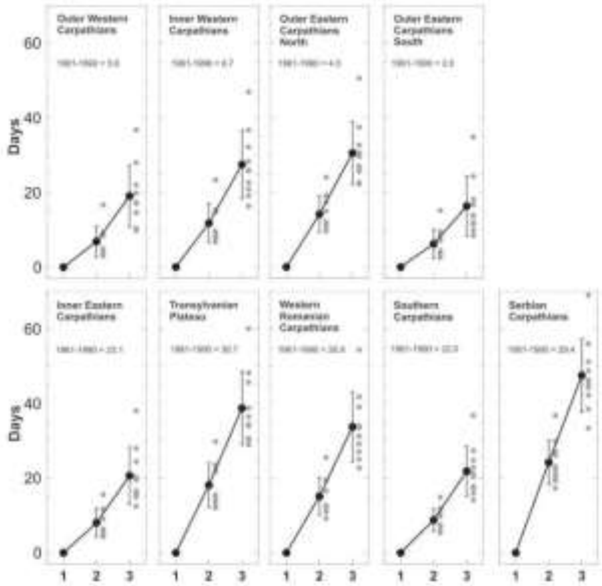


Fig. E6 Projection of the number of days with maximum daily air temperature exceeding 30°C based on 10 climate models

SUPPLEMENTARY MATERIAL F Values of maximum change in climate variables that underlie the calculation of aggregate climate change maps (equations are described in the paper)

Table F1 Maximum changes in climate variables used to identify climate change hot-spots according to the 10 climate models

Climate model	PTGS	EQ	T30	CDD	GSL
	(%)	(°C mm^{-1})	(No. of days)	(No. of days)	(No. of days)
Average of 10 RCMs	-31	+20	+58	-7	+41
RCA-ECHAM5	-28	+9	+55	-9	+40
HadRM3Q0-HadCM3Q0	-38	+31	+80	-8	+61
HIRHAM5-ARPEGE	-55	+35	+42	+10	+34
CLM-HadCM3Q0	-22	+23	+60	-5	+53
REMO-ECHAM5	-38	+30	+44	-8	+54
RACMO2-ECHAM5	-60	+37	+42	-9	+36
ALADIN-ARPEGE	-38	+19	+66	-8	+37
RCA-HadCM3Q0	-28	+10	+56	-8	+54
HIRHAM5-ECHAM5	-26	+11	+48	-8	+46
REGCM3-ECHAM5	-32	+16	+57	-8	+43

SUPPLEMENTARY MATERIAL G Aggregate climate change maps based on 10 climate models and climate change hot-spots

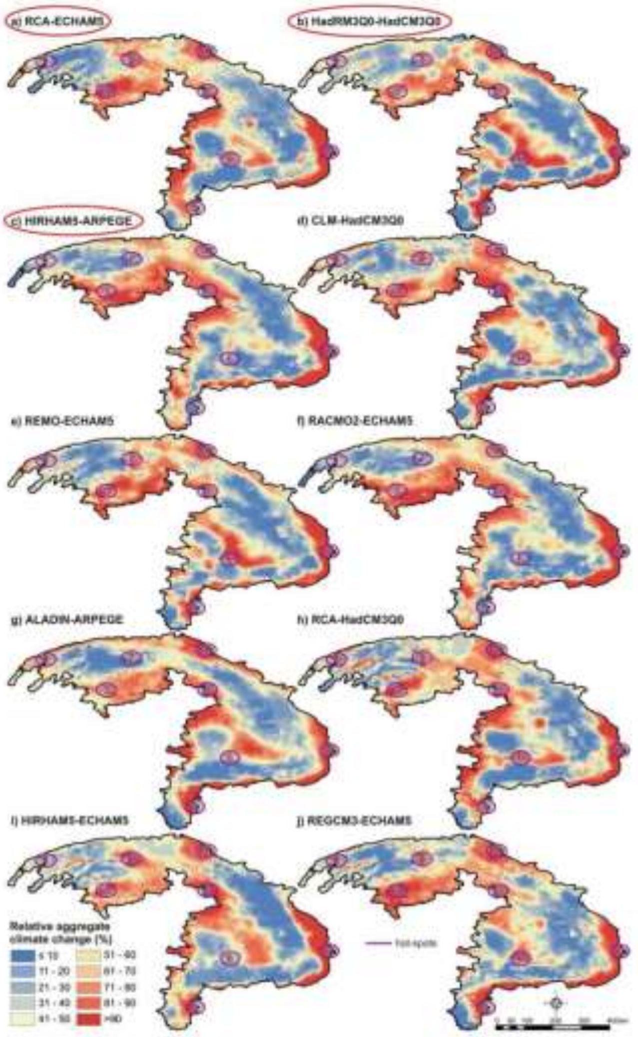


Fig. G1 Distribution of the residual aggregate climate change (i.e. aggregate climate change with extracted spatial trend) in the Carpathians based on the 10 climate models used in this study. Three contrasting climate models identified using the temperature-precipitation diagram in the Supplementary material C are highlighted (a,b,c). The displayed hot-spot positions are derived from the mean climate projection.

Codes of climate change hot-spots: 1 – CZ$_{HS}$; 2 –SK-PL$_{HS}$; 3 –SK-HU$_{HS}$; 4 – UA–North$_{HS}$; 6 – Trans$_{HS}$; 7 – RO–East$_{HS}$; 8 – RS$_{HS}$

SUPPLEMENTARY MATERIAL H Regions with the residual aggregate climate change above 70 % of the regional range

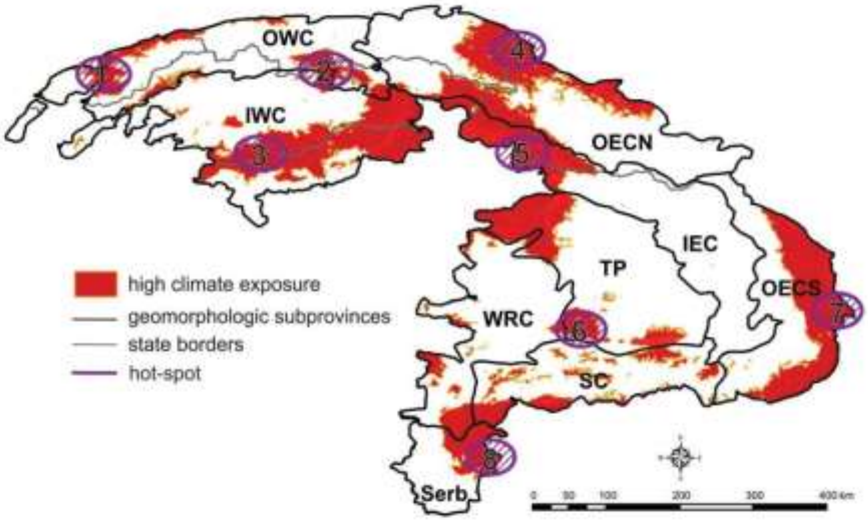


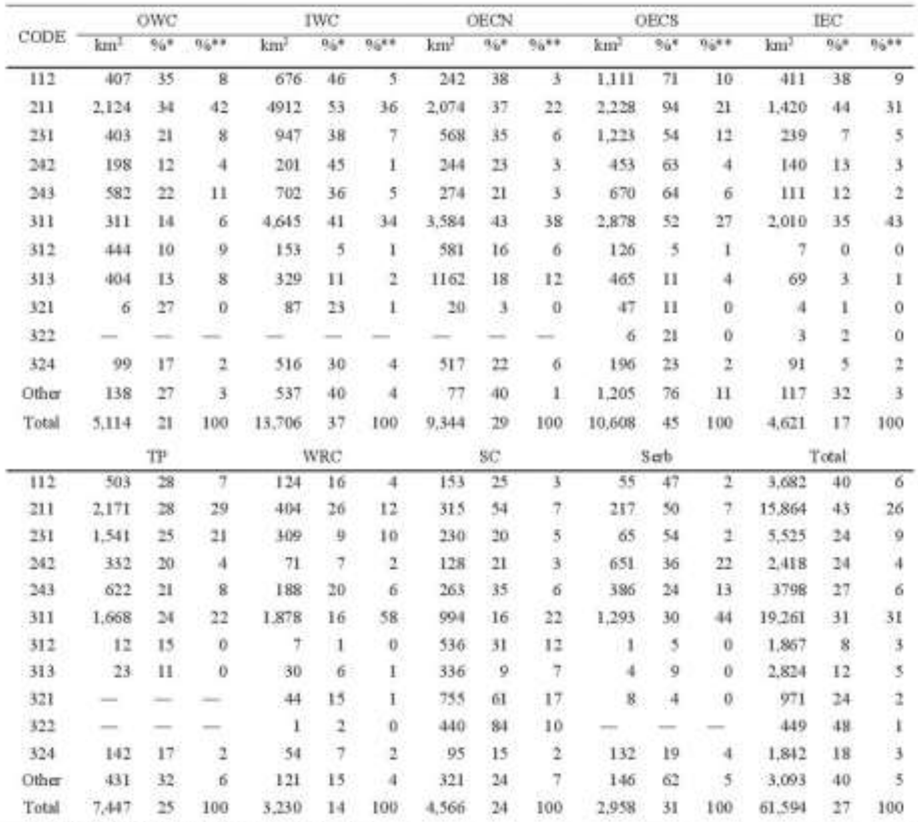
Fig. H1 Regions with climate exposure above 70 % quantile of the residual aggregate climate change and climate change hot-spots

Codes of geomorphologic units: OWC – Outer Western Carpathians; IWC – Inner Western Carpathians; OECN – Outer Eastern Carpathians North; OECS – Outer Eastern Carpathians South; IEC – Inner Eastern Carpathians; TP – Transylvanian Plateau; WRC – Western Romanian Carpathians; SC – Southern Carpathians; Serb – Serbian Carpathians

Codes of climate change hot-spots: 1 – CZ_{HS}; 2 –$SK\text{-}PL_{HS}$; 3 –$SK\text{-}HU_{HS}$; 4 – $UA\text{-}North_{HS}$; 6 – $Trans_{HS}$; 7 - $RO\text{-}East_{HS}$; 8 – RS_{HS}

The figure shows the residual aggregate climate change (ACC%) above the threshold of 70 % quantile. Such a threshold was used to identify the regions with high climate exposure relative to the rest of the region. Hot-spot positions are indicated as well.

SUPPLEMENTARY MATERIAL I Percentages of the main land cover types (EEA 2006) in climatically highly exposed regions in the Carpathians. The percentage of each category within the exposed regions and the percentage of the total category in the Carpathians are indicated. Only categories above 5% are presented



CODE	OWC			IWC			OECN			OECS			IEC		
	km^2	%*	%**	km^2	%*	%**	km^2	%*	%**	km^2	%*	%**	km^2	%*	%**
112	407	35	8	676	46	5	242	38	3	1,111	71	10	411	38	9
211	2,124	34	42	4912	53	36	2,074	37	22	2,228	94	21	1,420	44	31
231	403	21	8	947	38	7	568	35	6	1,223	54	12	239	7	5
242	198	12	4	201	45	1	244	23	3	453	63	4	140	13	3
243	582	22	11	702	36	5	274	21	3	670	64	6	111	12	2
311	311	14	6	4,645	41	34	3,584	43	38	2,878	52	27	2,010	35	43
312	444	10	9	153	5	1	581	16	6	126	5	1	7	0	0
313	404	13	8	329	11	2	1162	18	12	465	11	4	69	3	1
321	6	27	0	87	23	1	20	3	0	47	11	0	4	1	0
322	—	—	—	—	—	—	—	—	—	6	21	0	3	2	0
324	99	17	2	516	30	4	517	22	6	196	23	2	91	5	2
Other	138	27	3	537	40	4	77	40	1	1,205	76	11	117	32	3
Total	5,114	21	100	13,706	37	100	9,344	29	100	10,608	45	100	4,621	17	100

	TP			WRC			SC			Serb			Total		
112	503	28	7	124	16	4	153	25	3	55	47	2	3,682	40	6
211	2,171	28	29	404	26	12	315	54	7	217	50	7	15,864	43	26
231	1,541	25	21	309	9	10	230	20	5	65	54	2	5,525	24	9
242	332	20	4	71	7	2	128	21	3	651	36	22	2,418	24	4
243	622	21	8	188	20	6	263	35	6	386	24	13	3798	27	6
311	1,668	24	22	1,878	16	58	994	16	22	1,293	30	44	19,261	31	31
312	12	15	0	7	1	0	536	31	12	1	5	0	1,867	8	3
313	23	11	0	30	6	1	336	9	7	4	9	0	2,824	12	5
321	—	—	—	44	15	1	755	61	17	8	4	0	971	24	2
322	—	—	—	1	2	0	440	84	10	—	—	—	449	48	1
324	142	17	2	54	7	2	95	15	2	132	19	4	1,842	18	3
Other	431	32	6	121	15	4	321	24	7	146	62	5	3,093	40	5
Total	7,447	25	100	3,230	14	100	4,566	24	100	2,958	31	100	61,594	27	100

* Percent of the total category area in the Carpathians

** Percent of a category inside climatically highly exposed regions

Codes of geomorphologic units: OWC – Outer Western Carpathians; IWC – Inner Western Carpathians; OECN – Outer Eastern Carpathians North; OECS – Outer Eastern Carpathians South; IEC – Inner Eastern Carpathians; TP – Transylvanian Plateau; WRC – Western Romanian Carpathians; SC – Southern Carpathians; Serb – Serbian Carpathians

Codes of land cover types: 112 – Discontinuous urban fabric; 211 – Non-irrigated arable land; 231 – Pastures; 242 –Complex cultivation patterns; 243 – Land principally occupied by agriculture, with significant areas of natural vegetation; 311 – Broad-leaved forest; 312 – Coniferous forest; 313 – Mixed forest; 321 – Natural grasslands; 322 – Moors and heathland; 324 – Transitional woodland-shrub; Other – Other categories

SUPPLEMENTARY MATERIAL J Percentages of the main natural vegetation types (Bohn et al. 2004) in climatically highly exposed regions in the Carpathians. The percentage of each category within the exposed regions and the percentage of the total category in the Carpathians are indicated. Only categories above 5% are presented

CODE	OWC			IWC			OECN			OECS			IEC		
	km²	%*	%**	km²	%*	%**	km²	%*	%**	km²	%*	%**	km²	%*	%**
D37	—	—	—	—	—	—	100	2	1	34	1	0	—	—	—
F120	148	12	3	626	13	5	368	99	3	—	—	—	1,242	99	20
F125	299	20	6	236	92	2	2,997	41	28	220	16	2	801	18	13
F126			0	—	—	—	—	—	—	1,713	69	16	—	—	—
F135	676	10	13	207	4	2	5,302	33	49	724	10	7	—	—	—
F22	96	99	2	—	—	—	—	—	—	37	54	0	2,201	70	35
F58	1,870	40	37	3,769	50	27	477	34	4	—	—	—	1,145	100	18
F62	—	—	—	—	—	—	—	—	—	1,504	100	14	—	—	—
F64	—	—	—	—	—	—	—	—	—	4,153	83	39	—	—	—
G16	—	—	—	5947	68	43	—	—	—	—	—	—	—	—	—
U16	215	75	4	1,358	69	10	—	—	—	1,442	94	14	474	36	8
Other	1,811	26	35	1,563	20	11	1,569	70	15	783	92	7	373	30	6
Total	5,116	21	100	13,707	37	100	10,813	30	100	10,609	45	100	6,247	22	100
	TP			WRC			SC			Serb			Total		
D37	—	—	—	—	—	—	828	24	18	—	—	—	963	4	1
F120	—	—	—	—	—	—	—	—	—	—	—	—	2,385	31	4
F123	—	—	—	558	31	17	384	27	8	—	—	—	942	29	1
F124	—	—	—	348	34	11	447	95	10	609	26	21	1,403	36	2
F125	309	14	4	—	—	—	—	—	—	—	—	—	4,872	22	8
F126	224	6	3	327	9	10	82	7	2	—	—	—	2,346	19	4
F135	6	2	0	103	5	3	304	8	7	—	—	—	7,331	16	11
F22	1,028	78	14	—	—	—	—	—	—	—	—	—	3,362	70	5
F58	—	—	—	—	—	—	—	—	—	—	—	—	7,261	49	11
F62	—	—	—	—	—	—	—	—	—	—	—	—	1,504	100	2
F64	—	—	—	—	—	—	78	17	2	—	—	—	4,232	78	7
G16	1,840	79	25	297	12	9	—	—	—	—	—	—	8,085	58	12
G19	—	—	—	—	—	—	—	—	—	1,163	26	39	1,163	26	2
G20	25	100	0	442	23	14	197	66	4	8	21	0	673	29	1
G21	1,134	91	15	67	22	2	—	—	—	6	92	0	1,207	78	2
G3	838	12	11	64	95	2	—	—	—	—	—	—	901	13	1
G8	—	—	—	372	42	12	201	100	4	243	68	8	816	57	1
U16	878	35	12	270	21	8	275	69	6	—	—	—	4,913	53	8
Other	1,166	13	16	374	21	12	1,769	83	39	931	43	31	10.340	33	16
Total	7,448	25	100	3,231	14	100	4,567	24	100	2,959	31	100	64,696	28	100

* Percent of the total category area in the Carpathians

** Percent of a category inside climatically highly exposed regions

Codes of geomorphologic units: OWC – Outer Western Carpathians; IWC – Inner Western Carpathians; OECN – Outer Eastern Carpathians North; OECS – Outer Eastern Carpathians South; IEC – Inner Eastern Carpathians; TP – Transylvanian Plateau; WRC – Western Romanian Carpathians; SC – Southern Carpathians; Serb – Serbian Carpathians

Codes of natural vegetation types: D37 – East and South Carpathian spruce forests; F120 – Pre-Carpathian(-north Pannonian) beech forests; F123 – Moesian beech forests; F124 – Moesian silver lime-hornbeam-beech forests; F125 – Pre-Carpathian beech forests; F126 – Southeast Carpathian hornbeam-beech forests; F135– Carpathian fir-beech and spruce-fir-beech forests; F22 – Hercynian-pre-Carpathian hygrophilous pedunculate oak forests; F58 – North Pannonian-Carpathian sessile oak-hornbeam forests; F62 – East pre-Carpathian-Moldavian sessile oak-hornbeam forests; F64 – Southeast Carpathian sessile oak forests; G16 – Pannonian-pre-Carpathian sessile oak-bitter oak forests; G19 – Illyrian-west Moesian Balkan oak-bitter oak forests; G20 – Pannonian-Danubian Balkan oak-bitter oak forests; G21 – Danubian-east Balkanic mixed bitter oak forests; G3 – Transylvanian mixed Tatarian maple-oak forests; G8 – Pre-Carpathian mixed Oriental hornbeam-sessile oak forests; U16 – Pannonian-pre-Carpathian hardwood alluvial forests; Other – Other categories

SUPPLEMENTARY MATERIAL K Protected areas, NATURA 2000 sites and proportions of human population in climatically highly exposed regions in the Carpathians. Percent of the total category area/population in the Carpathians is given

CATEGORY	OWC		IWC		OECN		OECS		IEC		TP		WRC		SC		Serb		Total	
	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%
PROTECTED AREAS (Source: Carpathian Network of Protected Areas, www.carpathianparks.org; national environmental databases)																				
National park	78	22	732	18	747	22	—	—	—	0	—	—	71	10	430	29	496	80	2,554	22
Nature reserve	212	55	129	6	156	20	85	12	5	0	—	—	559	23	1,092	53	26	43	2,265	23
Protected landscape area	102	2	942	28	2,146	56	—	—	167	74	—	—	—	—	—	—	—	—	3,357	25
Total	392	6	1,803	19	3,048	38	85	12	172	7	—	—	630	20	1,522	43	523	77	8,176	23
NATURA 2000 SITES (Source: http://ec.europa.eu/environment/nature/natura2000/index_en.htm)																				
Birds Directive Sites SPA	178	6	3,975	37	1,996	48	1,046	55	487	9	860	19	821	17	880	26	29	44	10,273	27
Habitats Directive Sites pSCI, SCI, SAC	159	4	1,369	23	1,145	52	361	14	242	4	283	9	879	13	2,536	28	30	47	7,002	18
Sites proposed or designed under both Directives	23	50	—	—	406	36	—	—	—	—	—	—	—	—	—	—	—	—	430	32
Total	361	5	5,344	31	3,548	47	1,406	32	729	7	1,143	15	1,700	15	3,416	27	58	45	17,705	23
POPULATION (Source: Ruffini et al. 2006; Gallego 2010)																				
Total (thousands of inhabitants)	1,212	34	1,769	46	501	28	1,442	71	390	23	672	23	170	17	301	26	311	31	6,768	36

Codes of geomorphologic units: OWC – Outer Western Carpathians; IWC – Inner Western Carpathians; OECN – Outer Eastern Carpathians North; OECS – Outer Eastern Carpathians South; IEC – Inner Eastern Carpathians; TP – Transylvanian Plateau; WRC – Western Romanian Carpathians; SC – Southern Carpathians; Serb – Serbian Carpathians

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5.3 The first record of *Ips duplicatus* (Coleoptera: Curculionidae, Scolytinae) infestations in central european inner mountains.

THE FIRST RECORD OF *IPS DUPLICATUS* (COLEOPTERA: CURCULIONIDAE, SCOLYTINAE) INFESTATIONS IN CENTRAL EUROPEAN INNER MOUNTAINS*

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The natural distribution of the double-spined spruce bark beetle, *Ips duplicatus*, includes the Palearctic stretching from Scandinavia across NE and Central Europe to NE Asia. The first outbreak of I. duplicatus in Central Europe probably occurred in the early 1990s in North Moravia and Silesia, where the beetle still infests spruces at elevations < 600 m a.s.l. This species, which prefers elevations < 600 m a.s.l., has not been previously found within large mountain ranges. The present study, however, deals with I. duplicatus occurrence at ca. 600 m a.s.l. in two large mountain ranges – the Moravskoslezské Beskydy Mts. and the Hrubý Jeseník Mts. In both the regions, the beetle was detected in the terminal parts of closed valleys, approximately 20 km south of the infested sites at 400 m a.s.l. The new infestations at 600 m a.s.l. probably result from the increased abundance of the beetle in the lowlands of the closed valleys. The only defence currently known is to identify and harvest (destroy) the infested trees before offspring mature and overwinter in the litter. Occurrence of I. duplicatus within large mountain ranges constitutes a new risk for spruce stands in the mountains, at least in the Abieto-Fagetum forest vegetation (altitudinal) zone.

bark beetle; occurrence; infestation; spruce; Czech Republic

INTRODUCTION

The double-spined spruce bark beetle, *Ips duplicatus* (Sahlberg, 1836) (Coleoptera: Curculionidae, Scolytinae), is naturally distributed over the Palearctic stretching from Scandinavia across some parts of NE and Central Europe to NE Asia (Wood, Bright, 1992; Pfeffer, 1995). Until the 20th century, the southernmost occurrence of *I. duplicatus* in Europe was in the Bialowieza Primeval Forest in today's northern Poland. In the first half of the 20th century, however, *I. duplicatus* began to spread southwards into artificially established spruce stands both in lowlands and uplands (Pfeffer, Knížek, 1995). The first record of *I. duplicatus* in Central Europe came from southern Poland (Tredl, 1907; Karpiński, 1925, 1926). In the Czech Republic it was firstly recorded in the eastern parts (Wanka, 1927), its first occurrence in Slovakia was reported almost simultaneously (Roubal, 1941). In northern Austria the first observations of *I. duplicatus* fall within the 1980s (Holzschuh, 1989).

By the end of the 1990s, *I. duplicatus* became widespread both in Slovakia (Turčáni et al., 2001) and the Czech Republic (Holuša et al., 2010). Since 2005, the beetle' main occurrence shifted from the east south- and westwards into the central part of Bohemia (Holuša et al., 2010). The southern border of its central European distribution is likely to be in southern Slovakia (Zúbrik et al., 2006).

Pfeffer, Knížek (1995) stated that the first serious outbreak of *I. duplicatus* probably occurred in North Moravia and Silesia in the early 1990s. At that time, several hundreds of thousands of cubic metres of wood were harvested because of the beetle infestation. The volume of infested wood continued to increase because of the continuing effects of drought and *Armillaria* infestation (Knížek, 1998; Holuša, Liška, 2002). A similar *I. duplicatus* outbreak was recorded simultaneously in southern Poland (Grodzki, 1999).

Today, pheromone monitoring regularly detects *I. duplicatus* in highlands with elevations under 600 m a.s.l. (Holuša et al., 2006), and flying beetles are detected only exceptionally at higher elevations of the exterior ranges of the Western Carpathians (Holuša, 2004).

Currently no occurrence of *I. duplicatus*-infested trees is known in the interior parts of high mountain ranges, i.e., mountains exceeding 1,000 m a.s.l. (e.g.

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Kula, Ząbecki, 2001, 2002a, b). The present study focused on the determination of the current distribution of *I. duplicatus* in the eastern part of the Czech Republic in order to ascertain whether the beetle still occurs only at the foot of the mountains or whether the spruces in the interior parts of the Moravskoslezské Beskydy Mts. and the Hrubý Jeseník Mts. are also endangered.

MATERIAL AND METHODS

Characteristics of the study areas

Infested trees were studied at two localities in the Czech Republic (indicated by stars in Fig. 1):

(1) **Čeladná, Umučený** (49°27'24.712"N, 18°20'50.947"E; 660 m a.s.l.). Čeladná is located in the Moravskoslezské Beskydy Mts. (Outer Western Carpathians) and has an area of 623 km^2 and elevations between 508–1,323 m a.s.l. This locality supports the *Abies-Fagus*, *Picea-Fagus*, and *Fagus-Picea* forest vegetation (altitudinal) zones (for definitions, see Viewegh et al., 2003), with a dominance of the *Abies-Fagus* forest vegetation zone (Holuša, 2004). Spruce dominates the woody plants and represents ca. 80 % of the tree community mainly on non-original stands. Seven spruce (*Picea abies* L. (Karst.)) trees (38 m tall) were examined at this locality on August 15, 2012.

(2) **Adolfovice**, at the foot of Bezový Mt. (50°11'47.425"N, 17°9'22.939"E; 691 m a.s.l.). The locality is in the Hrubý Jeseník Mts. (Sudeten subprovince) and has an area of 530 km^2 and elevations between ca. 400–1,492 m a.s.l. The *Picea-Fagus* forest vegetation zone is dominant (covering 37 % of the area), and at higher elevations *Fagus-Picea* and *Picea* zones are abundant, covering 22 and 12 % of the area. The *Abies-Fagus* zone occupies 27 % of the lower boundaries of the area. Spruce stands of uniform age currently dominate the locality (occupying ca. 80% of the area), and a few stands have a substantial number of broadleaf trees, mainly beech (Culek 1996). Fifteen spruce trees (32 m tall) were examined at this locality on July 29, 2012.

Detection of *I. duplicatus*

In mature forest spruce stands at each study locality, spruce trees 25–35 cm in diameter (at chest height), older than 100 years, and with beetle infestation were cut down just above soil level. For assessment of bark beetle abundance, the entire trunk of each tree was debarked, and the extent of beetle infestation was assessed for each of the 1 m long sections. The width of each section (along the radial tree axis) was equal to half of the section's circumference. Beetles were considered abundant if there were more than 10 entrance holes per 0.1 m^2, and beetles were considered sparse if there were fewer than 9 entrance holes per 0.1 m^2. Stages of bark beetles were recorded, and bark beetles were identified to species based on adult morphology.

RESULTS AND DISCUSSION

I. duplicatus was detected at both localities. At Čeladná, all seven trees were infested with the bark beetles *Ips typographus* (L. 1758) and *Pityogenes chalcographus* (L. 1758). Two trees were abundantly infested ($>$ 10 entrance holes per 0.1 m^2) with *I. duplicatus*. Abundant infestation of the trunks from Čeladná extended from the height of 12.5 ± 0.7 m to 24.5 ± 0.7 m; the stems had developed galleries that contained L2–L3 larvae and maternal beetles. At Adolfovice, all 15 trees were infested with *I. duplicatus*, *I. typographus*, and *P. chalcographus*, but infestations of the latter two species were sparse. Abundant infestation of the trunks with *I. duplicatus* extended from the height of 8.8 ± 0.7 m to 27.9 ± 2.3 m; stems had developed galleries that contained L2–L3 larvae and maternal beetles.

Both localities were similarly situated, in the closed part the valley, ca. 600 m a.s.l., and were ca. 20 km south of the already infested sites at 400 m a.s.l. in the respective valleys (Fig. 1). The developmental stages of *I. duplicatus* detected were the same along the trunks at both localities.

Before the present study, *I. duplicatus* has never been detected within large mountain ranges. Recently, infested trees have been detected in flat to rolling highlands at elevations up to ca. 600 m a.s.l. (Turčáni, 2000; Holuša et al., 2010; personal observations). Although infested trees have occasionally been found in the Moravskoslezské Beskydy Mts. at 800 m a.s.l. (Holuša, 2003), these were growing on slopes adjacent to a lowland area. Contrarily, the infested trees under the present study were situated in closed valleys of extensive mountain ranges with elevations exceeding 1,000 m a.s.l.

The occurrence of *I. duplicatus* within extensive mountain ranges is probably a consequence of its increased abundance in the lowlands (Holuša et al., 2010) and pressures of a growing population along the longitudinal axes of the interior valleys. Both Čeladná and Adolfovice are in forest districts where only ca. 100 overwintering beetles per pheromone trap were captured as recently as 2011 (Knížek, Modlinger, 2012). This, however, is the consequence of their location within mountainous areas where densities of *I. duplicatus* have historically been low. In both areas, the first bark beetle infestations occurred in 2011. A longer-term local bark beetle outbreak exists on the southern slope of Smrk Mt. in the Moravskoslezské Beskydy Mts.; this outbreak including *I. typographus* and *Ips amitinus* (Eichhoff, 1872), is at 1,200 m a.s.l.

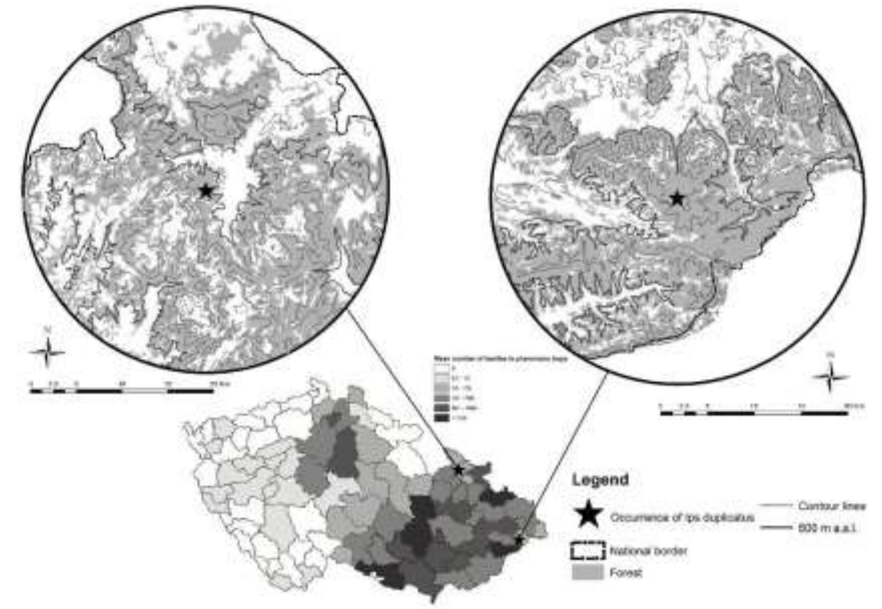

Fig. 1. Locations of Adolfovice (left) and Čeladná (right) (grey area – forest stands) in relation to pheromone monitoring of *Ips duplicatus* in the Czech Republic during 2011 (below, captures of the overwintering generation according to Knížek, Modlinger (2012))

and has been detected by trap trees (Lukášová, Holuša, 2011). The now infested standing trees were studied only in 2010, when infestation with *I. duplicatus* was not found (personal observation).

Both Čeladná and Adolfovice have elevations that only slightly exceed 600 m a.s.l., and detection of *I. duplicatus* at these localities is in accord with the beetle's preference for elevations ≤ 600 m a.s.l. (Grodzki, 2002, 2003; Vakula et al., 2011).

The rate at which *I. duplicatus* is multiplying and spreading in Central Europe indicates that this species has reacted positively to the moderate climate in Central Europe (Holuša et al., 2010). Although *I. duplicatus* is adapted to northern and possibly to mountain conditions, in response to higher temperatures it is capable of producing multiple generations per year. According to most authors, while this species annually produces one generation in the taiga and in northern Poland (Saalas, 1923; Karpiński, 1933; Pfeffer, 1955; Schnaider, Sierpiński, 1955), it produces up to three generations in Central Europe per year (Schnaider, Sierpiński, 1955; Grodzki, 1997; Holuša et al., 2003, 2006). Although *I. duplicatus* occurs at higher altitudes just sporadically (Grodzki, 2002, 2003; Holuša et al., 2010; Vakula et al., 2011), it resembles *I. typographus* here in producing only one generation per year (Holuša et al., 2006). At elevations like Čeladná and Adolfovice (600 m a.s.l.), *I. typographus* can produce 1–2 generations per year (Holuša et al., 2006). In the present study, the mature beetles detected were probably re-emerging maternal beetles (rather than a new generation of adults), which matches the general pattern observed at lower and medium elevations in Central Europe in 2012 (personal observation).

CONCLUSION

Although it has an extensive range, *I. duplicatus* is usually captured in pheromone traps at lower and medium elevations. In addition, the number of beetles captured in pheromone traps correlates with the number in infested trees (Holuša et al., 2010).

Control of *I. duplicatus* is complicated by several factors. First, *I. duplicatus* normally attacks scattered trees within a stand, and the invasion is concentrated in the tree crowns. Second, beetle development is often either completed or considerably advanced before change in needle colour is evident; i.e., infested trees are recognized only late. Third, *I. duplicatus* only rarely invades trees lying on the ground, and therefore classical traps cannot be used for its control (Grodzki, 1997; Knížek, 1998, 2010; Holuša et al., 2006). The only defence is to identify and harvest (destroy) infested trees before offspring mature and overwinter in the litter.

The occurrence of the double-spined bark beetle, *I. duplicatus*, in the interior of mountain ranges constitutes a new threat for spruce stands in the mountains, at least in the *Abies–Fagus* zone. On the basis of these findings, the recommendation is to monitore *I. duplicatus* with pheromone traps within mountain ranges and at elevations up to ca. 600 m a.s.l. If *I. duplicatus* is captured at these locations, we recommend that trees infested with bark beetles be debarked and studied in detail to confirm *I. duplicatus* occurrence. If the species of *I. duplicatus* is confirmed, foresters must carefully examine other trees in the area to determine the extent of the infestation and to guide management decisions.

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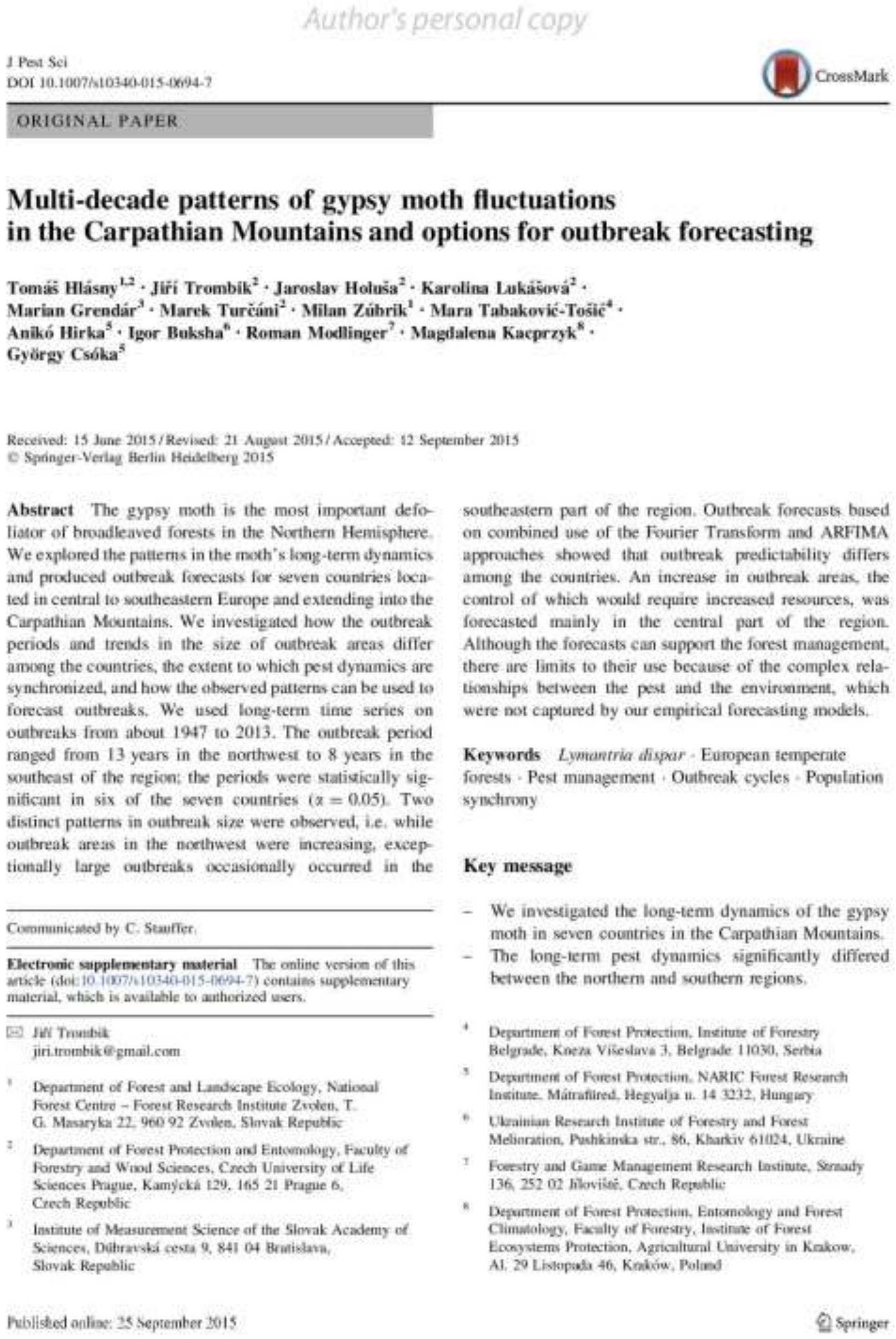
5.4 Multi-decade patterns of gypsy moth fluctuations in the Carpathian Mountains and options for outbreak forecasting.



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ORIGINAL PAPER

Multi-decade patterns of gypsy moth fluctuations in the Carpathian Mountains and options for outbreak forecasting

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Abstract The gypsy moth is the most important defoliator of broadleaved forests in the Northern Hemisphere. We explored the patterns in the moth's long-term dynamics and produced outbreak forecasts for seven countries located in central to southeastern Europe and extending into the Carpathian Mountains. We investigated how the outbreak periods and trends in the size of outbreak areas differ among the countries, the extent to which pest dynamics are synchronized, and how the observed patterns can be used to forecast outbreaks. We used long-term time series on outbreaks from about 1947 to 2013. The outbreak period ranged from 13 years in the northwest to 8 years in the southeast of the region; the periods were statistically significant in six of the seven countries ($\alpha = 0.05$). Two distinct patterns in outbreak size were observed, i.e. while outbreak areas in the northwest were increasing, exceptionally large outbreaks occasionally occurred in the southeastern part of the region. Outbreak forecasts based on combined use of the Fourier Transform and ARFIMA approaches showed that outbreak predictability differs among the countries. An increase in outbreak areas, the control of which would require increased resources, was forecasted mainly in the central part of the region. Although the forecasts can support the forest management, there are limits to their use because of the complex relationships between the pest and the environment, which were not captured by our empirical forecasting models.

Keywords *Lymantria dispar* · European temperate forests · Pest management · Outbreak cycles · Population synchrony

Key message

- We investigated the long-term dynamics of the gypsy moth in seven countries in the Carpathian Mountains.
- The long-term pest dynamics significantly differed between the northern and southern regions.

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- The outbreak period length was strongly controlled by geographical gradients, and pest populations were moderately synchronous.
- Future outbreaks are likely to increase in size in some countries and will require increased resources for control.

Introduction

The Carpathian Mountains, which pass through Austria, the Czech Republic, Slovakia, Poland, Hungary, Ukraine, Romania, and Serbia, contain the largest continuous forest ecosystem in Europe (Ruffini et al. 2006). Recently, forest damage in the Carpathians has increased (Hlásny and Sitková 2010; Badea et al. 2011) following the European-wide trend in forest disturbances (Schelhaas et al. 2003; Lindner et al. 2010; Seidl et al. 2014). Forest pests are climatically sensitive and are affecting forests worldwide (Bentz et al. 2010; Fisichelli et al. 2014). Recent climate effects, such as reduced tree resistance to pests and diseases (Malmström and Raffa 2000; Roy et al. 2004; Woods et al. 2005), modified developmental rates of some pests (Logan et al. 2003), expanded pest outbreak ranges (Parmesan et al. 1999; Vanhanen et al. 2007; Hlásny and Turčáni 2009, 2013), and increased abundances of some native pests that were previously considered unimportant (Netherer and Schopf 2010; Duduman et al. 2011), are expected to significantly alter the forests in the Carpathians.

One climate-responsive insect pest with Carpathian-wide distribution is the gypsy moth (*Lymantria dispar* L.) (Villemant and Fraval 1998; Csóka and Hirka 2009). The gypsy moth can feed on more than 300 tree species (Liebhold et al. 1995; McManus and Csóka 2007) and is one of the main defoliators of oak forests in Europe (Davidson et al. 2001; McManus and Csóka 2007). Feeding by gypsy moth caterpillars reduces the rate of tree growth (Naidoo and Lechowicz 2001), reduces seed production, weakens trees physiologically, and can even lead to tree death (Eisenbies et al. 2007; Tabaković-Tošić 2013).

Gypsy moth population dynamics are characterized by cyclical increases in abundance that result in the defoliation of large forest tracts (McManus and Csóka 2007; Tabaković-Tošić 2013). The outbreak period varies across geographical gradients (Weiser 1987; McNamara 1996), decreasing from the northwest to the southeast. The period is about ca. 12 years in central Europe but only 7–8 years in the Mediterranean and Balkan regions (Weiser 1987; Johnson et al. 2005); there are indications of sub-harmonic oscillations with period 3–4 years (e.g. Marović et al. 1998), which have been reported also from different environments (e.g. Bjørnstad et al. 2010).

A spatial synchrony of oscillation for geographically separated populations is a common characteristic of numerous insect populations and can inform the search for underlying mechanisms (Liebhold et al. 2004; Johnson et al. 2005; Haynes et al. 2013). The synchrony also suggests the extent to which the information on population dynamics and forecasts can be transferred between countries and regions. Although gypsy moth populations were found to be synchronized to a certain extent across large territories (Myers 1998; Peltonen et al. 2002; Johnson et al. 2005), factors influencing gypsy moth periodicity and geographical synchronization are unresolved (Johnson et al. 2005, 2006). There is evidence that population synchrony can be induced by environmental perturbations rather than by dispersal (Haynes et al. 2013). Weather patterns and gypsy moth populations were found to be synchronous at similar scales (Peltonen et al. 2002), suggesting that weather had a synchronizing effect by controlling gypsy moth survival and reproduction as well as by affecting pathogens and predators (Haynes et al. 2013). In particular, rainfall might increase gypsy moth mortality by enhancing the transmission of the gypsy moth nucleopolyhedrosis virus (LdNPV) (D'Amico and Elkinton 1995) or by enhancing infection by the fungus *Entomophaga maimaiga* (Entomophtorales: Entomophtoraceae) (Weseloh 1993). The effect of weather on the complex interactions between generalist predators and gypsy moth populations is also likely to enhance synchrony (Haynes et al. 2009).

When based on the relationship between pre-seasonal egg mass density and defoliation intensity, forecasts of gypsy moth outbreaks provide useful, short-term (about 1 year) predictions (Liebhold et al. 1993; Gribko et al. 1995). The ability to perform medium-term forecasting (i.e. to predict an outbreak several years into the future) is limited by the complex relationships between the pest and the environment (Wilder 1999) as well as by the biotic interactions (Dwyer et al. 2004; Bjørnstad et al. 2010; Haynes et al. 2013), and is made even more difficult by climate change. Pernek et al. (2008) suggested that the cyclical pattern of gypsy moth outbreaks and of climatic data can be used for short-term forecasting, although limits related to the questionable cycling of weather patterns are apparent (Martinat 1987; Burroughs 1992).

Given that the moth regularly damages forests and might expand to new territories under climate change (e.g. Vanhanen et al. 2007; Hlásny and Turčáni 2009), forecasting gypsy moth outbreaks and controlling moth damage are important and require a better understanding of the moth's long-term dynamics. In the current study, we attempted to increase the current knowledge of gypsy moth dynamics in the area surrounding the Carpathian Mountains by investigating the long-term time series of defoliation data collected by national forest protection services. The study adds to the research of Johnson et al. (2005) by focusing on a finer scale of regional outbreak areas rather than on a country-wide scale, and by drawing inferences about gypsy moth ecology and population dynamics that are specific to the Carpathian environment. We attempted to answer the following questions:

- Do data collected from the main outbreak areas in seven Carpathian countries reveal geographical patterns of population synchrony and outbreak period length that were not detected in previous studies (e.g. Peltonen et al. 2002; Johnson et al. 2005; Pernek et al. 2008; Cocco et al. 2010)?
- Do the long-term trends in the extent of gypsy moth outbreak areas indicate an increasing risk to the Carpathian forests?
- Can patterns of past gypsy moth outbreaks support outbreak forecasting?

To answer these questions, we tested the hypothesis that there is significant synchronization in gypsy moth populations in the Carpathians, where populations are separated by distances in which the synchronization is likely to occur (Myers 1998; Peltonen et al. 2002; Johnson et al. 2005). We also tested the hypothesis that outbreak extent and severity are increasing in time across the Carpathians and that the pattern of outbreak occurrence is sufficiently regular to facilitate a forecasting of future outbreaks. The results are intended to support pest management in that they should improve outbreak forecasting and should also increase our understanding of gypsy moth ecology and population dynamics in the Carpathians.

Data and methods

Historical records and recent distribution of the gypsy moth

We used the long-term annual records on gypsy moth-induced forest defoliation from seven countries, the territories of which extend into the Carpathians. These countries were the Czech Republic (CZ), Slovakia (SK), Poland (PL), Hungary (HU), Ukraine (UA), Romania (RO), and Republic of Serbia (RS).

The collected historical records cover the period from ca. 1947 to 2013, although the starting and ending years differ among the countries (Supplementary material A). The records include data on the annually defoliated area in hectares. For a limited number of recent outbreaks, the data were spatially referenced on the basis of countries' administrative districts. The latter information is used to identify the most distinct outbreak area in each country (Supplementary material B).

Periodicity

The periodicity of gypsy moth outbreaks was evaluated by the Fast Fourier Transform method (FFT). To meet the assumptions on the use of the FFT, each time series was log-transformed, a temporal trend was removed, and the resulting data were normalized to a mean of 0 and a variance of 1.0. A spectral density chart (periodogram) was used to identify the most distinct periodicities in each time series. The Normalized Fourier Power Spectrum (NFPS) was used to determine the significance of the identified peaks in each spectral density chart (Torrence and Compo 1998) at the level of 50, 95, and 99 %.

Forecasting

The FFT-based forecasting and Autoregressive Fractional Integrated Moving Average methods (ARFIMA) were used to forecast outbreaks. The former approach first determines outbreak frequency (number of outbreaks per unit time) and the number of components (i.e. periodic functions), and fits them to the observations. Then, amplitudes and phases of the used periodic functions are determined. Finally, such initial estimates are subjected to a non-linear optimization to improve the fit of the model to the data. Then, the forecast is produced by propagating the underlying periodic functions to the future.

Unlike the well-known ARIMA technique (Asteriou and Hall 2011), the ARFIMA models can capture the long-range dependences (LRDs) in a time series; such LRDs are characterized by a rate of decay of statistical dependence that is slower than an exponential decay. In our data, the presence of LRD was detected using the Hurst exponent H (Hurst 1951; Weron 2002) estimated by the Hipel and McLeod's method implemented in the R library FGN (Supplementary material C). A value of H in the range of 0.5–1.0 indicates the presence of LRD in the data. The ARFIMA model parameters were estimated using the maximum likelihood method (Haslett and Raftery 1989). The order of the model was determined using the step-wise procedure based on the statistical significance of the estimated parameters.

A quality of fit was evaluated for both models using the root-mean square errors normalized by the mean of observed values (RMSE%); in this case, the full length of the series was evaluated. For ARFIMA-based modelling, an additional test was done; the observed data were split into a parameterisation and validation set ($n = 10$), and the RMSE was calculated using the validation data. This procedure could not be applied in case of the FFT because the number of outbreak peaks in some time series was too small to allow the data to be split.

The stationary FFT-based approach was used only to forecast outbreak timing, while ARFIMA generated a complex outbreak pattern, including the trend in size of outbreak areas.

The AutoSignal (Systat Software Inc.) and the R language (R Core Team) library fracdiff (Fraley et al. 2006) were used for the above analyses.

Outbreak synchrony and trends

Because most synchrony metrics required that each time series contain the same number of records, the longest period for which the data were available in all countries, 1972–2010, was analysed. We evaluated the proportion of coincident peaks (C) (Yang and Rao 1993; Buonaccorsi et al. 2001) and correlation among time series using Spearman correlation (SP) (e.g. Adler 1994; Garber and Burger 1995) (Supplementary material D). Because the statistical significance testing of the SP can be violated by the autocorrelation pattern in the investigated time series, we used the block bootstrap procedure with blocks lengths based on the geometric distribution (Hall et al. 1995) to estimate the 95 % confidence intervals (CI) of each coefficient. The mean block size was indicated by the highest lag at which the autocorrelation coefficient was significant. The shape of the bootstrap distribution was used to choose the method for CI construction (i.e. normal approximation, basic bootstrap CI, percentile CI). The library boot in R (Canty and Ripley 2011) was used for the analysis.

Multi-decade trends in the size of defoliated areas were evaluated to identify the differences in outbreak development in individual countries. Logarithms of the original values were used to linearize the trends and to unify the scale of outbreaks. Both trends in the entire time series and in values related to outbreak peak years were evaluated. In the latter case, if a peak year could not be recognized, the average value of several adjacent years was used instead. Because of the temporal autocorrelation in the data, the modified Mann–Kendall test (Hamed and Rao 1998) was used to evaluate the significance of a monotonic trend in a time series. The R libraries fume and zyp were used for the analyses. Sen's slope (Sen 1968) was used as non-parametric estimation of the regression line slope. The median of residuals of observations from the Sen's slope was used to calculate the intercept (Rousseeuw and Leroy 2003).

Results

Synchrony in outbreak time series

The percentage of coincident outbreak peaks was highest between Slovakia and Poland (75 %), followed by Slovakia and Hungary (60 %), and then Romania and Serbia (57 %) (Supplementary material D). These pairs correspond with the adjacency of outbreak areas in these countries (Supplementary material B, D). Outbreak synchrony in terms of number of coincident peaks divided by the number of time series available in a given year differed over time (Fig. 1). While the level of synchrony was high from ca. 1945 to 1960 (although only three to four data series were available), the synchrony declined from 1960 to 1995. From 1995 to 2010, the synchrony recovered and reached its maximum in 2005, when the outbreaks occurred concurrently in all countries in the study region.

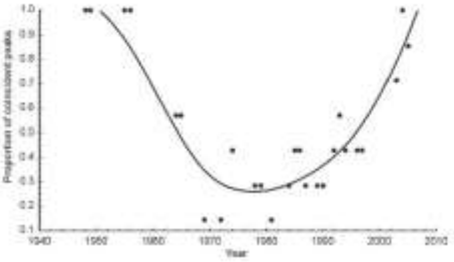


Fig. 1 Temporal development of the number of coincident outbreak peaks (1-year tolerance applied) divided by the number of available time series in each outbreak year. A distance-weighted least squares function was fitted to the data

Statistically significant values of SP ranging from 0.27 to 0.71 ($p < 0.05$) were found between 9 of 21 pairs of locations (Supplementary material D). The highest correlation was between Slovakia and Hungary (SP = 0.71; 95 % CI 0.53–1.0), followed by Hungary and Romania (0.52; 0.22–0.95), the Czech Republic and Slovakia (0.48; 0.11–1.0), and Romania and Ukraine (0.46; 0.25–0.70). All significant correlations are for paired locations that are within 700 km of each other, except for the correlation between Hungary and Ukraine (0.41; 0.09–0.74), where the paired locations are separated by 956 km.

A spatial pattern in outbreak synchrony was evaluated by plotting the SP against the distance that separated respective pairs of main outbreak areas. The coefficient decreased with increasing separation distance ($r^2 = 0.19$, $p = 0.047$, $t = -2.13$), suggesting that outbreak synchrony shows positive spatial autocorrelation (Fig. 2). While the linear trend reached a value of zero for SP at a distance of 1250 km, the lower CI (95 %) reached zero at 860 km; this is the distance at which the spatial synchrony of gypsy moth populations in the Carpathians disappears.

Periodicity in outbreak time series

According to FFT analysis, the outbreak period ranged from 8 to 13 years; the identified periods were statistically

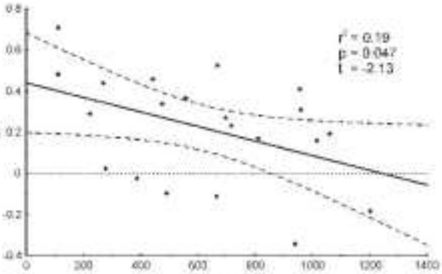


Fig. 2 Values of Spearman coefficient (SP) calculated between the pairs of outbreak time series (defoliated hectares) plotted against the distance that separates the pairs of time series. *Dashed lines* represent the 95 % confidence intervals

significant at $p < 0.05$ in six of the seven countries (Fig. 3). The longest outbreak periods were 12.5 and 13.0 years and were in Poland and the Czech Republic, respectively, where the main outbreak areas are located in the northwest of the study area (Supplementary material B). The statistically significant outbreak period with a value of 9.8 years was identified in both Slovakia and Hungary, where the outbreak areas are adjacent to each other. Ukraine, Romania, and Serbia, whose main outbreak areas are located in the southeast of the study area, had shorter outbreak period of ca. 8 years; however, the peak identified for Ukraine (7.7 years) was not statistically significant. The statistically significant period of 35.4 years in Ukraine is most likely a mathematical artefact that lacks ecological meaning.

Geographical pattern in outbreak cycles

The relationship between outbreak period and latitudinal and longitudinal gradients was evaluated with and without data from Ukraine, for which the periodogram peak was not statistically significant (Fig. 3). Geographic coordinates at the centres of main outbreak areas (Supplementary material B) were used as independent variables.

The outbreak cycles showed a strong geographical pattern, i.e. the period decreased from the northwest towards the south and east of the study region (Fig. 4). When period from Ukraine was excluded, the latitudinal and longitudinal gradients explained 63 and 84 %, respectively, of the variability in period length; when period from Ukraine was included, these values were 65 and 83 %, respectively. The combined effect of these variables accounted for 85 % without UA ($p = 0.06$) and 83 % with UA ($p = 0.02$) of the total variability. The data indicated that the outbreak period decreased by 1 year as latitude changed by ca. 1.5° to the south and as longitude changed by 3° to the east. The equations with and without data from Ukraine (Eq. 1 and 2, respectively) were as follows:

$$\text{Period} = -10.408 - 0.161x + 0.500y, \qquad (1)$$

$$\text{Period} = -21.899 - 0.003x + 0.679y, \qquad (2)$$

where x is latitude and y is longitude.

Long-term trends in the size of outbreak areas

The exploratory analysis of country-specific trends in the logarithms of areas defoliated in outbreak peak years showed great differences among countries (Fig. 5). While outbreak area increased in a group of countries in the northwest of the study region (i.e. the Western Carpathian countries Poland, Czech Republic, and Slovakia; Fig. 5a), the outbreak area showed no trend or tended to decrease in the southeastern countries (Ukraine, Romania, and Serbia; Fig. 5b). Although the trend was constant in Hungary, the non-parametric trend function based on Sen's slope did not reflect the last outbreak of unprecedented size in 2005, which could be indicative of an increasing trend. The Mann–Kendall test showed that the significant increasing monotonic trend was present only in the SK time series ($p = 0.089$) (Table 1).

Regarding detection of trends in the entire time series (i.e. not only in the peak years), the Mann–Kendall test showed no significant trend in either country (Table 1). However, this calculation was affected by the large number of zero values in the inter-outbreak periods. The trend in entire model region (all countries summed) was also not significant ($p = 0.93$) (Fig. 5b).

Outbreak forecasts

Based on the complete time series (not the validation set only), the variability of residuals was higher for the ARFIMA (RMSE% 88–169) than for the FFT (32–65 %) (Fig. 6; Table 2); this difference was mainly due to the lower variability of the log-transformed data used in the FFT-based forecasting. For both forecasting methods, the fit (in terms of rank) was better for Romania and Ukraine than for the Czech Republic, Hungary, and Serbia. For Slovakia and Poland, the quality of the fit differed between the methods.

When the ARFIMA models were tested using the validation data (the last 10 observations), the RMSEs calculated for the parameterization and validation data were approximately of the same magnitude for Romania, Ukraine, Serbia, and Poland, suggesting that the models have good forecasting performance in these countries. This was not the case for the remaining countries, where the

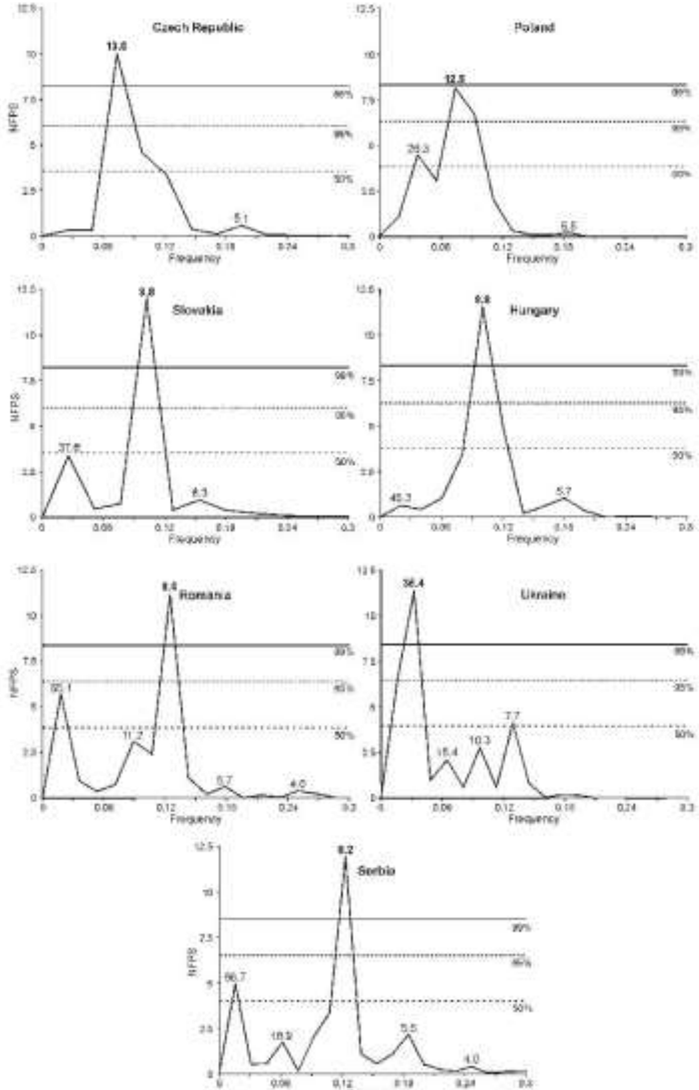


Fig. 3 Frequency periodograms of gypsy moth outbreaks in seven countries that extend into the Carpathian territory. *Horizontal lines* indicate the 50, 95, and 99 % significance levels determined using the Normalized Fourier Power Spectrum (NFPS). Frequency units on the *horizontal* axis are inversely proportional to the period (frequency = 1/period in years). Years are shown at periodogram peaks; *bold numbers* represent statistically significant periods

RMSEs calculated for the parameterization and validation data differed substantially.

The consistency of forecasts produced by the two models can be considered a useful indicator of forecast reliability and applicability; such a conservative approach may lead, in some cases, to the reconsideration of the applicability of seemingly reliable forecasts based on single models.

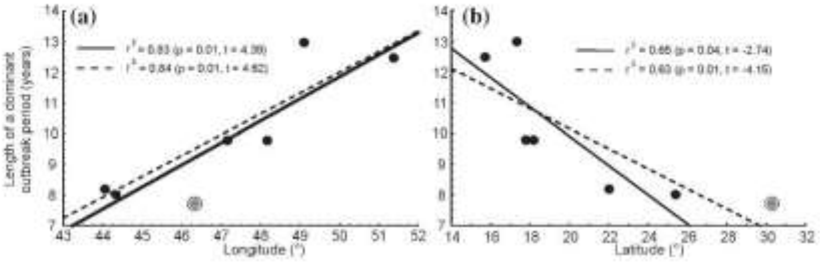


Fig. 4 The relationship between gypsy moth outbreak period (the duration of the interval between outbreaks) and longitudinal (**a**) and latitudinal (**b**) gradients. *Solid line* without the period from the Ukraine, which was statistically insignificant (*grey symbol*); *dashed line* all countries considered (*black points*)

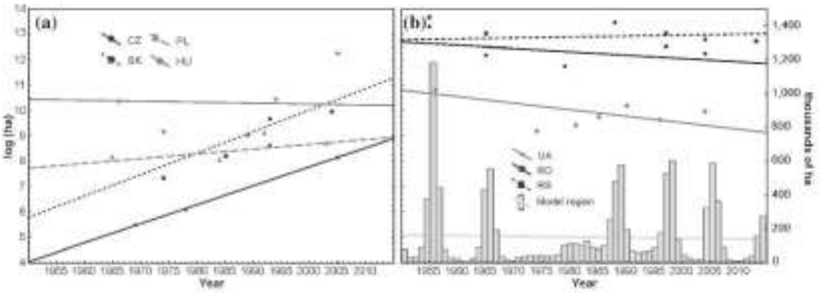


Fig. 5 Trends in the logarithms of areas defoliated in outbreak peak years in seven countries that extend into the Carpathian territory. Pane **a** shows countries in the central to northwestern region, and pane **b** shows countries in the southeastern region (the *Y*-axis to the *left*). *Bars* in pane **b** show defoliated areas (ha) summed over the entire model region (the *Y*-axis to the *right*)

In the Czech Republic, the peaks forecasted by the two methods were apparently asynchronous, even though the models fit the recent two outbreaks very well. This finding should reduce the confidence in single-model forecasts; moreover, RMSE% of both models and RMSE of the ARFIMA model had high values, indicating poor model performance.

In Poland as in the Czech Republic, the poor match of the two forecasts suggested poor applicability; while no apparent peak was forecast by the FFT for Poland, two sharp peaks were forecast by the ARFIMA. Because the RMSE produced using the validation data suggested that the ARFIMA performed well; however, this forecast might be preferred.

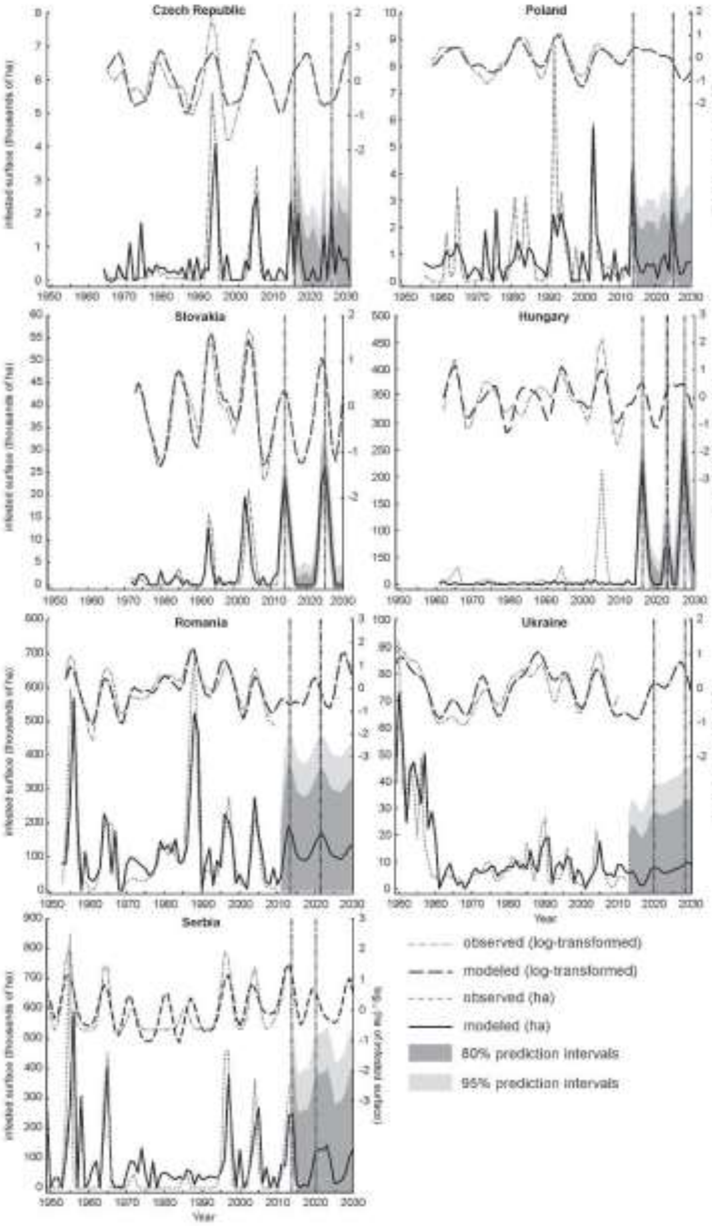
In Slovakia and Hungary, both forecasts were relatively consistent, although the RMSE and RMSE% were not optimal in either dataset. However, an extreme difference between the RMSE calculated for the parameterisation and validation data in Hungary is related to the extreme size of the very recent peak used for the validation; it follows that the forecast should not be discarded on the basis of this value. In the view of such an ambiguous evaluation, we suggest considering the good match of the two forecasting models as the superior indicator of forecast reliability.

Table 1 The statistical significance of the monotonic increasing or decreasing trend in outbreak time series evaluated using the Mann–Kendall test

Country	Mann–Kendall test values	
	A	*B*
Czech Republic	0.31	0.20
Poland	0.73	0.12
Slovakia	0.09	0.63
Hungary	0.46	0.75
Romania	1.00	0.98
Serbia	0.45	0.74
Ukraine	0.71	0.16

The trends in both the outbreak peak years (*A*) and entire time series (*B*) are evaluated

In Romania, two forecasted peaks occurred almost simultaneously in both forecasts. In Ukraine, both forecasts


Czech Republic
Poland
Slovakia
Hungary
Romania
Ukraine
Serbia
infested surface (thousands of ha)
log10 (ha of infested surface)
Year
observed (log-transformed)
modeled (log-transformed)
observed (ha)
modeled (ha)
80% prediction intervals
95% prediction intervals

◂**Fig. 6** The forecasts of gypsy moth outbreaks in the Carpathian countries based on the Fast Fourier Transform method and the ARFIMA. The *vertical lines* indicate how the outbreak peaks forecasted by the two methods match

indicated that an outbreak is likely to occur in 2020, although the peaks are relatively indistinct. In both countries, this agreement between forecasts along with relatively low values for RMSE and RMSE% suggests that these forecasts can be thought of as reliable.

The inter-model agreement in outbreak timing was also high in Serbia, although the RMSE% of both models was high. However, the RMSE based on the validation set was almost equal to that based on the parameterization data, what suggests that these forecasts can be thought of as reliable.

In addition to forecasting outbreak timing, the ARFIMA models also predicted the size of outbreak areas, with obvious limitations. The clearly increasing trend with relatively narrow prediction intervals was forecasted for Slovakia and Hungary (see also Fig. 5). In Ukraine, the outbreak areas are likely to increase as well and may substantially exceed the extent of defoliation observed in the last 50 years. In the remaining countries, no trend was apparent, and the forecasted areas did not exceed the areas reported in the past decades.

Discussion

Our study has provided fundamental information on gypsy moth dynamics in those countries in central and southeastern Europe whose borders extend into the Carpathian Mountains. The investigated long-term time series of gypsy moth outbreaks showed a moderate level of synchrony and diverging long-term trends in outbreak areas, and strong latitudinal and longitudinal control over the outbreak periods. In the following paragraphs, we discuss how our findings increase the understanding of gypsy moth ecology and population dynamics, and the implications for pest management and forecasting.

Observed synchrony and periodicities

We found positive correlations between time series from adjacent outbreak areas and the strength of the correlation declined with increasing distance between the outbreak areas. This is consistent with previous studies. Peltonen et al. (2002), for example, reported that gypsy moth populations in the northeastern USA are synchronous up to 600 km. Johnson et al. (2005) found a significant synchrony in the Northern Hemisphere populations up to a distance of 1,200 km according to spatial covariance analysis, but the synchrony was significant up to a distance of 600 km according to wavelet phase analysis. Although our study cannot be directly compared with these earlier studies because different methods were used, the measure of synchrony used in our study had declined to zero at a distance between 860 and 1260 km. The coefficient linearly decreased as the distance separating the paired outbreak time series increased, which is consistent with the intra-continental evaluation by Johnson et al. (2005). Such findings suggest that the linear decrease of synchronization with increasing distance between populations, and the disappearance of the synchrony at a distance of up to 1300 km, may be a common regional-scale pattern; for example, Johnson et al. (2005) found an asymptotic pattern at an inter-continental scale.

The outbreak period showed a strong geographical pattern, with periods ranging from 13 years in the Czech Republic (in the northwest of the study region) to 7.7 years in Ukraine and 8.0 years in Romania (both in the southeast of the region); this range in period values agrees well with the previous studies of Johnson et al. (2005), Pernek et al.

Table 2 Root-mean square error (RMSE) calculated using the observed and simulated data for the size of areas infested by the gypsy moth

Country	FFT		AFRIMA			
	RMSE*	RMSE%*	RMSE*	RMSE%*	RMSE (*P*)**	RMSE (*V*)**
Czech Republic	0.50	64.66	701	168.91	2045	34,226
Poland	0.28	48.45	1169	137.84	1282	1087
Slovakia	0.27	32.13	3356	136.80	4539	53,541
Hungary	0.49	63.37	17,458	143.03	14,598	52,905
Romania	0.36	41.38	89,773	77.30	93,773	131,380
Ukraine	0.32	49.75	11,129	88.78	11,543	8387
Serbia	0.46	59.33	133,559	156.69	143,056	107,709

* The calculations were based on the full lengths of the used times series and are expressed in terms of the RMSE normalized by the mean of observed values (RMSE%)

** For ARFIMA, the RMSE was also calculated for the validation (*V*) and parameterization (*P*) data set

(2008), and Cocco et al. (2010). At the same time, longitudinal and latitudinal gradients explained ca. 85 % of variability in the period of outbreak cycles, and outbreak period declined linearly as the latitude moved south and as longitude moved east. Such a response of periodicity to a latitudinal gradient has also been recognized for other lepidopteran forest pests (e.g. Klemola et al. 2002; Cooke and Lorenzetti 2006).

In the view of the observed gradient in outbreak period, the exceptional synchronization of the outbreak in 2003–2005 in all countries in the study region seems surprising. A closer look, however, suggests that this synchrony can have a mathematical rather than an ecological explanation. When the interval between outbreak cycles identified in this study was added to the peak year of the previous observed outbreaks (1993–1998, depending on country), the resulting years ranged from 2003 to 2005 in all cases. Contrary to the suggestion of some authors (e.g. Myers 1998; Hawkins and Holyoak 1998), this indicates that no environmental trigger was needed to induce the synchronization and that some instances of synchrony may occur by chance. Such apparent synchronization also occurred in 1955, 1965, and 1974, although only three to four peaks coincided. Johnson et al. (2005) suggested that two outbreaks with cycle periods of 8 to 12 years have a probability of ca. 18 % to coincide by chance during seven outbreak cycles. That prediction of chance of synchrony, however, is extremely low in view of our data; we observed one coincidence of seven outbreak peaks and several coincidences of three to four peaks during a 60-year period. This suggests that either an effective but currently unrecognized synchronizing factor acts in our study region or that the probability of outbreaks co-occurring by chance should be reconsidered. Although 36 % of the outbreak peaks (the average of all pairwise comparisons) coincided in our study, the number of peaks in our series was relative small, and so inferences must be cautious.

Implications for forest management

The ability to predict gypsy moth outbreaks is limited by the complex relationships between the pest and its environment (Johnson et al. 2005, 2006) and by the unclear effects of management on pest population dynamics (Allstadt et al. 2013). Anyway, forest management may benefit from forecasts that narrow the range of potential forest development trajectories (Kimmins et al. 2010). The empirical forecasts based on the propagation of past fluctuation patterns used in this study have significant limits, which are particularly pronounced under changing environmental conditions. Our ability to generate more sophisticated forecasts is especially restricted by our insufficient understanding of the fundamental ecological processes that trigger outbreaks and that affect population synchronization.

Our study suggests that the predictability of outbreak incidence significantly differs among the countries. Ambiguity in the interpretation of forecasted patterns was enhanced by our conservative approach, i.e. we combined two independent forecasts for each country. That the patterns identified by the two methods often disagreed indicated that forecasts based on only one forecast model should be accepted with caution. When the two forecast models agreed, however, our confidence in the forecasts was increased. Valle et al. (2009) suggested in this regard that multi-model inference circumvents the problem of overly confident predictions or inferences by improving the representation of model structure-related uncertainty.

In the Czech Republic and Poland (the northwestern boundary of the Carpathians), where the gypsy moth has yet to cause significant damage, the high values for RMSE% and RMSE and the lack of agreement between the forecasts indicated that the forecast models have limited applicability in these countries. That outbreaks in the higher latitudes of Central Europe are likely to be fuelled by climate change (Logan et al. 2003; Vanhanen et al. 2007; Hlásny and Turčáni 2009), however, may increase the need for a reliable forecasting system in this region. For example, the possibility for improving the country-specific forecasts using the outbreak time series from neighbouring countries, which were found to be synchronized, should be explored. In Slovakia and Hungary, where the gypsy moth has been historically causing significant damage, the forecasts were relatively satisfactory, including relatively narrow prediction intervals. Hence, the forecasted outbreak timing could be cautiously used for assembling the resources needed for control.

The forecasts in the southeastern part of the study area performed relatively well (especially in Romania and Serbia), even though the observed outbreak patterns were highly irregular. Despite the statistically successful fitting and forecasting, the forecasts should be viewed with caution because specific patterns in observed data such as the irregular incidence of extreme outbreaks or the long latency period in Serbia are currently not understood and sufficiently captured by the forecasting models. We advise that the forecasts could be used cautiously for planning the resources for outbreaks suppression, though limits related to forecasts' empirical nature are apparent.

The complexity of forecasted patterns also suggested that naive forecasting based on the propagation of identified outbreak periods (the method of analogy), which is commonly used in forestry, can provide confusing outputs. Although this approach can seemingly provide useful information, it oversimplifies reality and may lead to incorrect forestry decisions or to ecologically implausible inferences.

While forecasts of outbreak timing can benefit from the regularity in observed data, forecasts of outbreak extent (i.e. area affected) are hampered by factors that are only poorly captured by a statistical forecasting model. Still, the current results indicate that outbreaks in the central to northwestern part of the study region, which includes some broadleaved forests that have not experienced outbreaks, will increase in area; this increase may presumably be accelerated by an increase in air temperature (Vanhanen et al. 2007; Hlásny and Turčáni 2009). Hlásny and Turčáni (2009) suggested that the current gypsy moth outbreak areas in Slovakia may enlarge significantly in response to the projected temperature increase and that gypsy moth can colonize the entire host plant range in the country with a temperature increase of ca. 2 °C. Although gypsy moth expansion might be limited by the distributional range of the main host plants (*Quercus* spp.) in the study region, the pest has already been observed to feed extensively on broadleaved hosts other than those that have frequently supported outbreaks (Csóka and Hirka 2009). Moreover, drought-adapted tree species such as oaks may benefit from climate change in Central Europe and expand their ranges, both naturally (Hlásny et al. 2011; Hanewinkel et al. 2012) and through the support of adaptive forest management (Lindner et al. 2010; Hlásny et al. 2014). Such expansion can lead to the formation of new outbreak spots. On the other hand, the possibility of climate change-mediated collapse of the long-term fluctuation cycles, which has been observed in some species (Ims et al. 2008; Johnson et al. 2010), should also be considered; to our knowledge, however, there is currently no indication of a climate change-mediated collapse in gypsy moth outbreak cycles. The recent emergence of the pathogen *E. maimaiga* in the Carpathian countries (Georgiev et al. 2012; Tabaković-Tošić et al. 2012; Zúbrik et al. 2014) is likely to reduce the amplitude of outbreak cycles because the fungus seems able to constantly elevate the mortality rates of the gypsy moth (Allstadt et al. 2013). However, the pathogen should have a little impact on the oscillation cycles driven by the interaction of gypsy moth populations with LdNPV (Liebhold et al. 2013).

In the southeastern part of the investigated region, where the long-term trends are for outbreak areas to remain stable or even to decrease in size, and where outbreaks with exceptional size occur irregularly, the options for forecasting outbreak size are limited. We do not expect the current outbreak areas to enlarge substantially (or to exceed the extent of the largest observed outbreaks) because most of the current distribution of host plants in the region is already within the area affected by outbreaks. In addition, outbreak suppression by increasing temperatures is unlikely because the gypsy moth can tolerate high temperatures (Keena 1996; Vanhanen et al. 2007). Thus, the pattern of "difficult to predict, extreme outbreaks" can be expected to persist in the future.

Conclusions

Our findings reveal substantial spatial and temporal variability in gypsy moth outbreak patterns and a moderate degree of outbreak synchronization in the region surrounding the Carpathians. Our findings also show that outbreak period in this region is strongly related to geographical gradients. The long-term trend in the size of outbreak areas was found to differ among the countries and indicated the potential for increasing damage to forests in the central to northwestern part of the Carpathians. In the southeastern part of the region, the long-term trends in outbreak areas were insignificant and irregular occurrence of outbreaks with exceptional size is a pattern typical of this region. Despite a remarkable variability in the available outbreak time series and differences in forecast applicability between the countries, the used forecasting approaches allowed us to predict future outbreak peaks; such predictions can help managers anticipate the resources needed for pest suppression. Although the presented forecasts should be useful, they must be viewed with caution and periodically reconsidered because future outbreaks could be enhanced by climate change or suppressed by the emerging pathogens.

Author contribution statement

TH designed the research and wrote the text. JT, MG analysed the data. JH, KL, MT co-wrote the text. MZ, MT-T, AH, IB, RL, MK, GC prepared the data. All authors read and approved the manuscript.

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Multi-decade patterns of gypsy moth fluctuations in the Carpathian Mts. and options for outbreak forecasting

SUPPLEMENTARY MATERIAL

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SUPPLEMENTARY MATERIAL A: Country-specific gypsy moth dynamics

Tab. A1 Description of the historical records on gypsy moth defoliation in the Carpathian countries used in the current study

Country	Period	Source	Reference
CZ	1964–2013	Forestry and Game Management Research Institute, Strnady, Czech Republic	Forest Protection Service, Database on forest damage agents (internal data)
SK	1972–2008	Forest Research Institute, Zvolen, Slovakia	Annual forest damage reports (internal data)
PL	1956–2013	Forest Research Institute, Sękocin Stary, Poland	Annual forest damage reports (internal data)
HU	1961–2012	Hungarian Forest Damage Database maintained by the Forest Research Institute Mátrafüred, Hungary	Annual forest damage reports and forecast (1961-2012) (internal data)
UA	1947–2012	Ukrainian Research Institute of Forestry & Forest Melioration, Kharkov, Ukraine	Statistical data of State Forest Resources Agency of Ukraine (internal data)
RO	1953–2010	Forest Research and Management Institute, Brasov, Romania	Tomescu and Netoiu (2006); Simionescu et al. (2001, 2011)
RS	1947–2013	Institute of Forestry, Belgrade, Serbia	Marović et al. (1998); Tabaković-Tošić and Jovanović (2007); Tabaković-Tošić 2013)

In the Czech Republic, the historical data were available for the period 1964–2013, covering four outbreak cycles. The largest outbreaks were recorded in 1994–1996 and 2002–2006, when 5,600 and 3,400 ha of oak forests were infested, respectively. Four cycles were recorded also in Poland during period 1956–2013, with the most severe outbreak in 1991–1995, when approximately 9,000 hectares were infested. In both countries, the gypsy moth has relatively minor role in forest disturbance regime.

Gypsy moth importance is much higher in Hungary and Slovakia (Zúbrik 2006; McManus and Csóka 2007; Csóka and Hirka 2009). This is expected to be mainly due to a warmer climate and larger proportion of host trees as compared with the earlier mentioned countries. Five cycles with increasing extent were reported in Slovakia during the period 1972–2013 (Leontovyč et al. 1980; Zúbrik et al. 2013). In the previous period, there are notes on outbreaks in 1948–1949 (Hendrych 1962) and 1955–1956 (Pfeffer 1961; Patočka et al. 1999), however, as only the descriptive information was available, these outbreaks were not included in the analysed time series. The most recent outbreak occurred during period 2003–2006, peaking in 2004. Approximately 50,000 hectares of mostly oak stands (*Quercus cerris* L., *Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) and poplar (*Populus* sp.) were defoliated. In Hungary, 5 cycles were reported during the period 1961–2012. The most recent outbreak (2003–2006) reached an unprecedented dimension of ca. 212,000 ha (McManus and Csóka, 2007). Extensive defoliation of host plants other than the primary host (*Q. cerris* and *Q. robur*) occurred, and also sessile oak (*Q. petraea*), European beech (*Fagus sylvatica* L.), native and hybrid poplars (*Populus sp.*), alder (*Alnus* sp.), black locust (*Robinia pseudoacacia* L.) and even some conifers (*Picea abies* (L.) Karsten, *Pinus sp.*) were defoliated (Csóka and Hirka 2009).

In Ukraine, 7 outbreak cycles were recorded during the period 1947–2012. The largest extent of defoliated forests was observed during the outbreak in 1948–1951, which peaked in 1949 and spread over 90,000 ha of forests dominated by *Q. robur*. Since 1960, extent of outbreak areas has remained more or less stable (15,000–20,000 ha in each peak year).

Six large-scale outbreaks were observed in Romania during the period 1953-2010. The largest outbreak occurred in 1987–1988, and reached 700,000 ha. More than 250,000 ha were reported as strongly defoliated (Tomescu and Netoiu 2006); the definition of strong defoliation is however not available in the source material.

In Serbia, the historical data were available for the period 1946–2014, covering eight cycles (Marović et al. 1998; Tabaković-Tošić and Jovanović 2007; Tabaković-Tošić 2013). Three subsequent outbreaks, which occurred during the period 1947–1966, were followed by the latency stage lasting for three decades, when only minor defoliations were reported in 1970–1973 and 1984–1987 (Marović et al. 1998). An exceptional outbreak spreading over 850,000 ha occurred in 1955 and spread across most of the country.

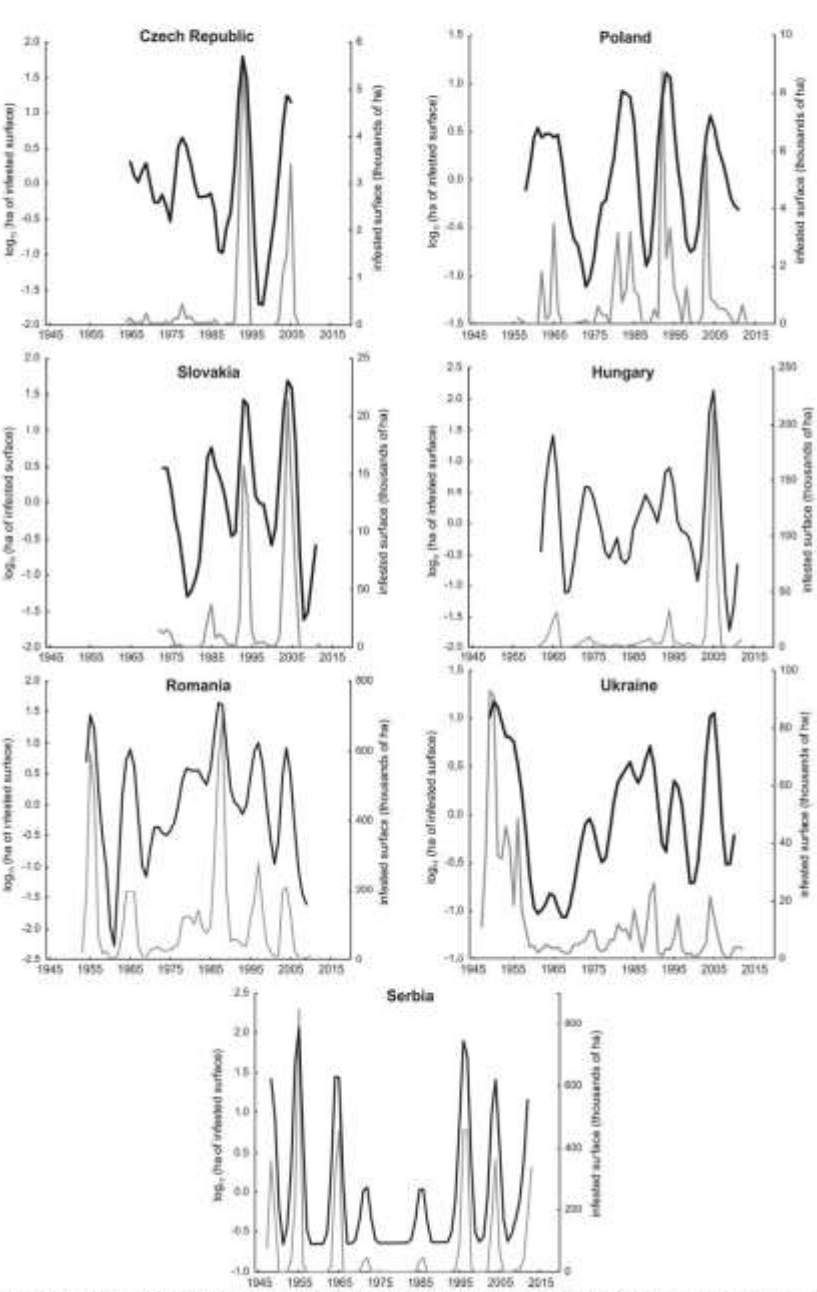


Fig. A1 Time series of defoliated areas (black line, Y-axis to the right) in the Carpathian countries and log-transformed data (grey line, Y-axis to the left)

SUPPLEMENTARY MATERIAL B: Main outbreak areas of the gypsy moth

To facilitate the analysis of spatial patterns in gypsy moth fluctuation as well as to provide the spatially explicit information on gypsy moth distribution, we identified the centre of the most distinct outbreak area in each country. We used the data on defoliation distribution within administrative districts, which were available during a limited number of recent outbreaks as well as using the historical descriptive information available at national forest protection services (Fig. A1). In the Czech Republic, the main outbreak area has relatively limited size with minor inter-outbreak differences during the recent 4 outbreaks. It covers the lowland oak forests (*Q. robur*, *Q. petraea*) at country's south-western border. In Poland, the main outbreak area lies in south-western part of the country and covers lowland oak forests (*Q. robur*, *Q. petraea*). In Slovakia, main outbreak area covers Turkey oak (*Q. cerris*) forests in lowland to foothill areas, mainly in the southern and south-eastern border of the country. In Hungary, outbreaks regularly occur across most of the country. Main outbreak area with highest intensity of defoliation lies in the central to western part of the country, in the Veszprém county, north of the Lake Balaton, where the caterpillars feeds mostly on Turkey oak and pedunculate oak (*Q. robur*). In Romania, the main outbreak area was defined by administrative districts in which the most intensive outbreaks were occurring in the period 1990-2010 (Simionescu et al., 2001, 2011). The area contains mostly oak forests of *Q. cerris* and *Quercus frainetto* Ten. in elevations ranging from ca 20-200 m a.s.l. In Ukraine, the Odesa district (southern part of the country) was identified as region with the highest intensity of outbreaks (Meshkova 2002). The area covers mainly *Q. robur* and other hardwood species in elevation 15-280 m a.s.l. In Serbia, most of outbreaks occurred in the vicinity of the Serbian Carpathians (Marović et al. 1998; Mihajlović 2008) in the forests of *Q. cerris* and *Q. frainetto*. An exception is the outbreak which culminated in 1965 and occurred, with minor intensity, across most of the country.

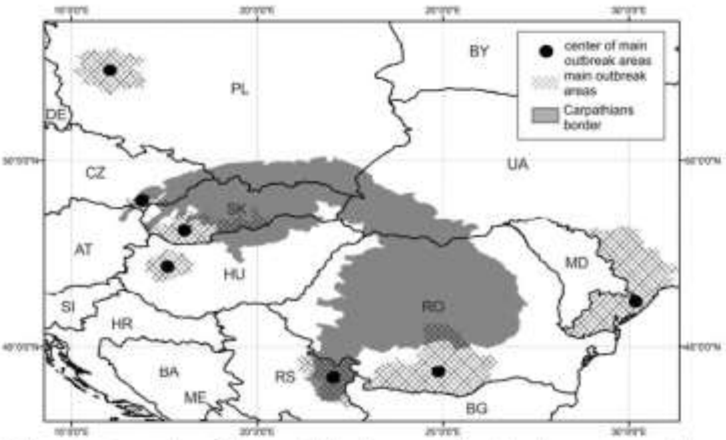
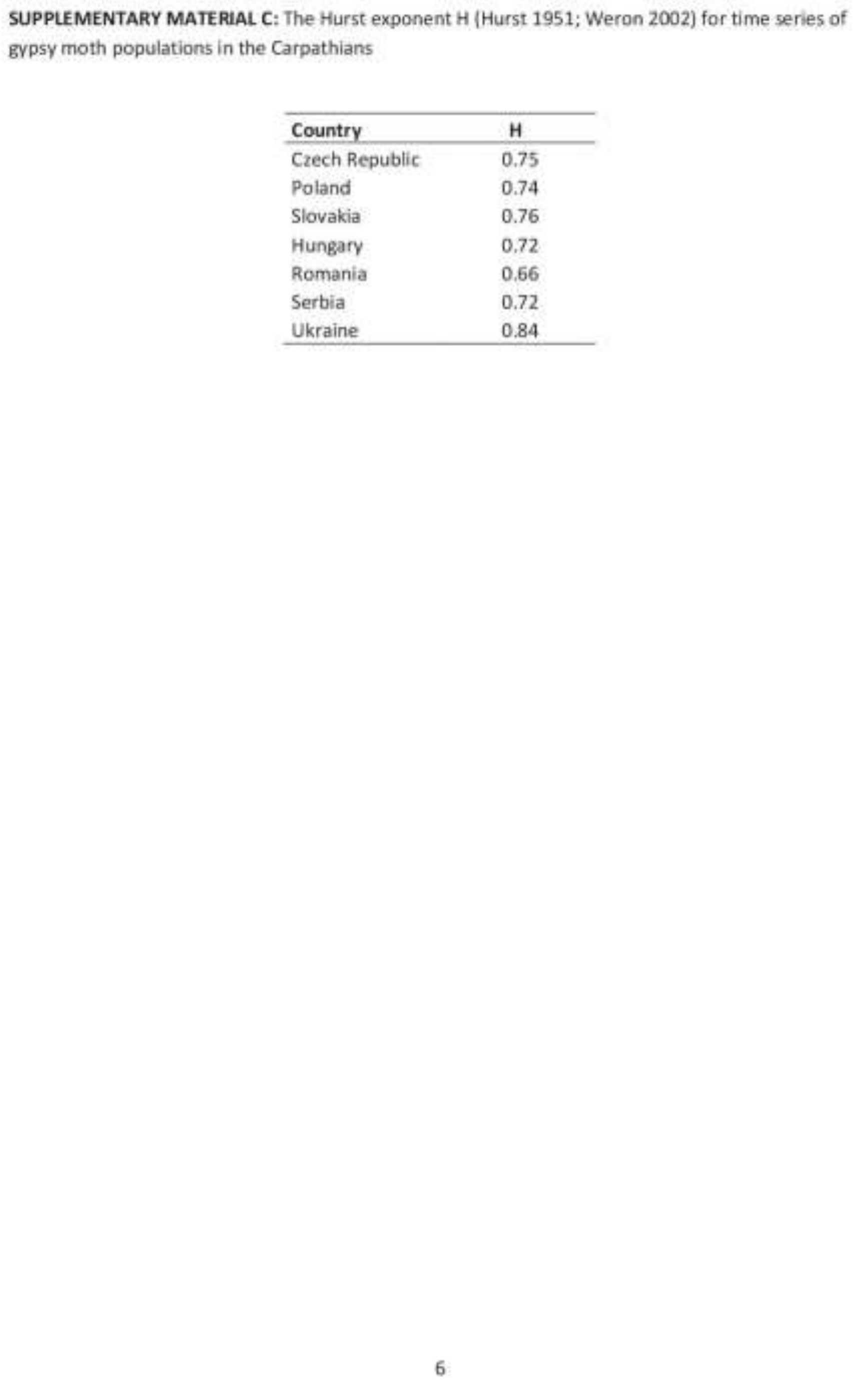


Fig. B1 Approximate centres of the most distinct gypsy moth outbreak areas in countries, which extend into the Carpathian Mountains. Outbreak area sizes are not comparable among the countries as they indicate just a rough position of the most infested regions to be used as a spatial reference of the outbreak time series to facilitate the spatially explicit analyses.



SUPPLEMENTARY MATERIAL C: The Hurst exponent H (Hurst 1951; Weron 2002) for time series of gypsy moth populations in the Carpathians

Country	H
Czech Republic	0.75
Poland	0.74
Slovakia	0.76
Hungary	0.72
Romania	0.66
Serbia	0.72
Ukraine	0.84

SUPPLEMENTARY MATERIAL D: Measures of synchrony of gypsy moth populations in the Carpathians

Tab. D1 Measures of synchrony of all pairs of defoliation time series used in the current study Abbreviations: SP – Spearman correlation with the 95% confidence intervals constructed by the block bootstrap procedure; N – number of coincident peaks; C – proportion of coincident peaks out of all time series available; Distance – distance between the centres of main outbreak areas identified for each country. Bold – statistically significant values ($p < 0.05$)

Series	SP	N	C	Distance (km)
CZ-SK	**0.48** [0.11; 1.32]	2	0.50	112
SK-HU	**0.71** [0.54; 1.00]	3	0.60	112
CZ-HU	0.29 [-0.07; 0.79]	2	0.40	220
RO-RS	**0.44** [0.18; 0.78]	4	0.57	271
CZ-PL	0.02 [-0.35; 0.33]	2	0.50	276
SK-PL	-0.02 [-0.37; 0.27]	3	0.75	388
UA-RO	**0.46** [0.25; 0.70]	2	0.29	443
HU-RS	**0.34** [0.14; 0.55]	2	0.29	476
PL-HU	-0.10 [-0.42; 0.17]	1	0.20	492
SK-RS	**0.37** [0.06; 0.72]	2	0.29	558
CZ-RS	-0.11 [-0.45; 0.21]	1	0.14	665
HU-RO	**0.52** [0.22; 0.95]	3	0.50	667
UA-RS	**0.27** [0.10; 0.46]	4	0.57	696
SK-RO	0.23 [-0.28; 0.95]	1	0.17	718
CZ-RO	0.17 [-0.29; 0.63]	2	0.33	809
PL-RS	-0.34 [-0.60; -0.12]	2	0.29	939
HU-UA	**0.41** [0.09; 0.74]	2	0.29	956
SK-UA	0.31 [-0.09; 0.74]	2	0.29	960
CZ-UA	0.16 [-0.32; 0.79]	1	0.14	1,014
PL-RO	0.19 [-0.06; 0.46]	2	0.33	1,061
PL-UA	-0.18 [-0.49; 0.07]	1	0.14	1,201
Mean	0.22	2	0.36	–

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5.5 Sustainable forest management in a mountain region in the Central Western Carpathians, northeastern Slovakia: the role of climate change.

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ORIGINAL ARTICLE

Sustainable forest management in a mountain region in the Central Western Carpathians, northeastern Slovakia: the role of climate change

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Abstract European forestry is facing many challenges, including the need to adapt to climate change and an unprecedented increase in forest damage. We investigated these challenges in a Norway spruce-dominated mountain region in Central Europe. We used the model Sibyla to explore forest biomass production to the year 2100 under climate change and under two alternative management systems: the currently applied management (CM), which strives to actively improve the forest's adaptive capacity, and no management (NM) as a reference. Because biodiversity is thought to have mostly positive effects on the adaptive capacity of forests and on the quality of ecosystem services, we explored how climate change and management affect indicators of biodiversity. We found a differential response across the elevation-climatic gradient, including a drought-induced decrease in biomass production over large areas. With CM, the support of non-spruce species and the projected improvement of their growth increased tree species diversity. The promotion of species with higher survival rates led to a decrease in forest damage relative to both the present conditions and NM. NM preserved the high density of over-matured spruce trees, which caused forest damage to increase. An abundance of dead wood and large standing trees, which can increase biodiversity, increased with NM. Our results suggest that commercial spruce forests, which are not actively adapted to climate change, tend to preserve their monospecific composition at a cost of increased forest damage. The persisting high rates of damage along with the adverse effects of climate change make the prospects of such forests uncertain.

Keywords European temperate forest · Forest disturbances · Forest management · Sibyla model · Climate change adaptation

Introduction

Future forest development has been increasingly considered during recent decades (e.g., Matala et al. 2003; Hlásny et al. 2011, 2014a; Lindner et al. 2014), and forest modeling tools have been substantially improved (e.g., Millington et al. 2011; Huber et al. 2013; Wang et al.

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2014). Such interest has been fueled by changing environmental conditions (Alessandri et al. 2014), by the increasing societal demand for sustainable multifunctional forestry (Gustafsson et al. 2012; Simoncic et al. 2013), by changes in the forestry institutional framework (Mendes et al. 2011), and by a growing body of evidence on changes in long-term forest dynamics (Boisvenue and Running 2006; Klapwijk et al. 2013; Pretzsch et al. 2014; Seidl et al. 2014). Indeed, standard management and planning tools, which obviously assume that climate and other conditions remain constant (Guariguata et al. 2012), can fail to provide reliable support to forest managers under such transient conditions. Instead, sophisticated forest models, often connected with decision support systems, have been adopted to support complex decisions under social and environmental uncertainty (Marušák and Kašpar 2015; Uhde et al. 2015).

European mountain forests provide an exceptional diversity of ecosystem services (ESs), including the provisioning of timber, fuel wood, food, natural hazard protection, water and air quality regulation, biodiversity maintenance, and a range of cultural services (Körner and Ohsawa 2005; Briner et al. 2012, 2013). Research has increasingly demonstrated that ESs are generated from numerous interactions in forest ecosystems (Gamfeldt et al. 2013, Harrison et al. 2014) and that the quality of ESs is closely related to biodiversity (e.g., Díaz et al. 2006). Traits such as species richness, abundance, and diversity showed predominantly positive relationship to wood production (Paquette and Messier 2011) or atmospheric, water, and pest regulation (Harrison et al. 2014). Moreover, increased species mixture may increase the survival of some tree species (Griess et al. 2012), which can be particularly important in forests with elevated disturbance rates. A support to forest diversity can also increase a forest's inherent adaptive capacity (Lindner et al. 2014) through enhanced compensatory dynamics between species (Morin et al. 2014).

Researchers have increasingly recognized the sensitivity of European mountain forests to climate change and to the concomitant changes in the social and economic environments (Elkin et al. 2013; Huber et al. 2013; Hlásny et al. 2011, 2014a). Because climatic effects are strongly driven by latitudinal and altitudinal gradients (Jump et al. 2009; Mátyás et al. 2010), mountains can exhibit a diversity of positive and negative responses. While mountain forests under climate change may benefit from a prolonged growing season and a reduced period with frozen soil (Bergh and Linder 1999; Jarvis and Linder 2000), forests in foothills and drier mountain valleys may suffer from drought (Rebetez and Dobbertin 2004; Jump et al. 2009). Particularly in Central Europe, an increased water scarcity interacting with climate-sensitive pest dynamics has been recognized as the most significant climate change-related threat to forests (Bolte et al. 2009; Lindner et al. 2010). The importance of this threat is underscored by the recent drought-induced dieback of forests worldwide (Allen et al. 2010) including Central Europe (Mátyás et al. 2010). At the same time, an increased concentration of atmospheric CO_2 can have a fertilizing effect that may increase tree productivity and water stress tolerance, although this effect can differ depending on site, tree dimensions, and other factors (Huang et al. 2007; Way 2011).

In recent centuries, Norway spruce [*Picea abies* (L.) Karsten] has been extensively planted in many regions of Europe to meet the growing demands of regional industries (Spiecker et al. 2004; Hlásny and Sitková 2010). Such secondary, low-diversity forests are prone to diverse kinds of damage (Badea et al. 2004) and can be sensitive to the direct effects of climate change (Hlásny et al. 2011, 2014b; Tatarinov et al. 2011) and particularly to climate change-mediated alterations of forest disturbance regimes (Seidl et al. 2008; Hlásny and Turčáni 2013). The transformations of the even-aged single-species forestry to alternative silviculture systems in many European countries (Puettmann et al. 2015) are particularly important in such forests because such transformations can increase such forests' resilience and inherent adaptive capacity.

The current study was conducted in a mountainous region containing forests that are representative of secondary spruce forests in many European countries (Spiecker et al. 2004; Hlásny and Sitková 2010; Hlásny and Turčáni 2013). The forest management in the region has been challenged by the long-term elevated activity of forest pests, the adverse effects of increased climatic variability (including large-scale windthrows), or the emerging need to adapt to the ongoing climate change. We evaluated the prospects of forest biomass provisioning, which accounts for ca. 95 % of the regional forestry economy. Because biodiversity is closely associated with the quality of most ESs and with the inherent adaptive mechanisms of ecosystems, we explored how biodiversity indicators will develop along with the simulated biomass production. We also compare forest development driven by the current management system (CM) with no management (NM) in order to identify the potential assets and deficiencies of CM. In support of these objectives, we tested the following hypotheses:

- Most indicators will respond differently to climate change in warm-dry and cool-wet species range limits (e.g., Hlásny et al. 2011; Elkin et al. 2013; Zlatanov et al. 2015), indicating the need to consider such a gradient in forest management planning and adaptation;

- The two management systems (CM and NM) will have remarkably different effects on indicators of biodiversity and biomass production;
- The anticipated positive effect of CM on tree species diversity and biomass provisioning will be significantly countered by the negative effects of climate change.

This study brings new information on the anticipated effect of climate change on intensively managed spruce forest in relatively understudied environment of Central European mountain ranges. The results obtained are expected to increase our understanding of interactions between climate and managed forests, which is a topic of growing importance for forestry as well as for climate change mitigation.

Data and methods

Study region

The Goat Backs Mts. model region is located in north-eastern Slovakia (Central Europe) in the mountain range of the Central Western Carpathians (Supplementary material A). The region covers an area of 8226 ha with 62.4 % forest cover and an altitudinal range of 650–1555 m a.s.l. The forests in this region include even-aged stands of Norway spruce (81.5 %), European larch (*Larix decidua* Mill.) (10.9 %), pine (*Pinus sylvestris* L.) (3.1 %), and silver fir (*Abies alba* Mill.) (1.7 %), with minor occurrences of European beech (*Fagus sylvatica* L.), sycamore (*Acer pseudoplatanus* L.), and blue spruce (*Picea pungens* Engelm.). Forest management in the region is described in the Supplementary material A.

Forest dynamics model

The forest dynamics model Sibyla (Fabrika and Ďurský 2005) is an empirical, individual tree-based, distance-dependent forest growth and yield model based on the SILVA model (Pretzsch et al. 2002). To make it representative of Central Europe, the model was parameterized using 1189 forest plots from the Slovak forest monitoring network established in 1994 (National Forest Centre, internal data) with spacing 4 × 4 km and plot size 500 m^2. The natural regeneration module was parameterized using the data from National Forest Inventory conducted in 2005–2006 in a regular grid of 4 × 4 km, containing 1486 circular forest plots with radius 12.62 m (Moravčík et al. 2010). The natural regeneration rate is driven by tree-specific seed production and quality parameters, stand density, and site parameters. It is only indirectly sensitive to climate through the modified development of the main forest stand.

The model simulates tree inherent mortality (i.e., mortality not induced by disturbances), which is controlled by stand density, tree competition, and site index that is responsive also to climate (Ďurský et al. 1996; Ďurský 1997). The effect of disturbances is simulated using species- and age-specific survival probabilities (Supplementary material D). The dead wood decomposition rates used in the model are based on Hlásny et al. (2014a).

Tree growth in the model is controlled by five temperature- and precipitation-related variables, soil moisture, nutrition, and atmospheric CO_2 and NO_x concentration (Kahn 1994; Pretzsch and Kahn 1998). Species-specific functions define the optimum range for each variable and are combined using the algorithm proposed by Kahn (1994) to modify a theoretical maximum tree growth at a given site.

Stem dimension (height and diameter) is the main state variable simulated by the model. Species-specific functions are used to derive the crown dimensions, timber volume, and biomass content in all pools. A suite of diversity indices are calculated using the data on tree positions and dimensions.

The model was validated in a number of stands using measured tree height and diameter data (Hlásny et al. 2011, 2014a; Bošeľa et al. 2013). While the model performed well under optimal site conditions, it failed to simulate forest dynamics under extreme conditions, particularly at xeric sites and at sites with extreme intra-annual temperature ranges. Such results are consistent with the testing of the original model SILVA in Switzerland (Schmid et al. 2005). It follows that the model is likely to perform well in Central European mountain regions, including the region of the current study, where the climate is moderate. That the model has not been tested against extreme climate events may limit its applicability in climate change research, which is an obvious deficiency of most vegetation dynamics models (e.g., Anderegg et al. 2015). While the climate change scenarios used in the current study predict only slight changes in the annual temperature amplitude (Supplementary material F), the simulations driven by the most extreme climate change scenario, which is likely to induce rather xeric conditions (Supplementary material C), should be interpreted cautiously.

Forest development drivers

Five climate change scenarios and a statistically generated stable climate corresponding to the period 1961–1990 were used to drive the forest development simulations. The used scenarios, which were selected from the 22 scenarios developed in the ENSEMBLES project (van der Linden and Mitchell 2009), cover the uncertainty range of the original data set. Observed climate data collected from 19 meteorological stations during the period 1961–2009 were used for scenario downscaling and for the creation of a stable (baseline) climate. While the projected temperature increase by the end of the century (2071–2100) ranges from 1.9 to 4.9 °C, the precipitation change ranges from +10 to −35 % of the baseline climate (Supplementary material C). More details on the climate data used can be found in Bugmann et al. (2015).

The IPCC SRES A1B scenario (Nakicenovic and Swart 2000) was used to describe the future development of CO_2 emissions, with a peak concentration of 717 ppm in 2100. We used increasing nitrogen deposition by Dentener (2006). The content of soil nutrients was derived from the forest soil maps of the region and was not subjected to any changes during the simulation period (Supplementary material B).

Simulation design

Representative stand types

The simulations were run in 25 so-called representative stand types (RSTs), which are the stands selected using the criteria specified in Supplementary material B to be representative of main stand types and site conditions in the study region. The information collected in a field survey conducted in 2011 was used to define the initial design of all RSTs in the used model. Sample plots with size 0.045 ha were established in each of the 25 preselected forest stands with three sample plots per ha. Tree heights and diameters, ratio of dead and living trees, regeneration density, and other stand characteristics were measured. Then, diameter class distribution, height curves, and other data collected in sample plots were used to designate the RSTs with size 200 × 12.5 m (0.25 ha) in the model. Such a shape was required to facilitate the simulation of harvesting operations, which are applied in parallel strips. Because information on tree positions was not available, we generated the initial design of each RST 15-times with different tree distributions so as characteristic species mixture patterns observed in the stands were preserved.

Simulation setup and evaluation

The management is implemented in the simulator in terms of the prescribed ages, diameter classes, and proportions of stocking volume to be extracted in individual years of the simulation period. Both natural and artificial regeneration modules are activated during the simulation; the artificial regeneration rates are given in Supplementary material B. To mimic the harvesting procedure used in the region (see Supplementary material A), the harvesting is simulated in 3–4 strips 40–60 m wide (based on the mean stand height). The edge effect is corrected using the linear expansion-based approach (Martin et al. 1977). Both tree inherent mortality and mortality related to forest disturbances are activated during the simulations. To cope with a limited knowledge of future disturbance regimes, we assumed that the future rate of forest damage remains equal to the calibration period 1998–2009 (Supplementary material D).

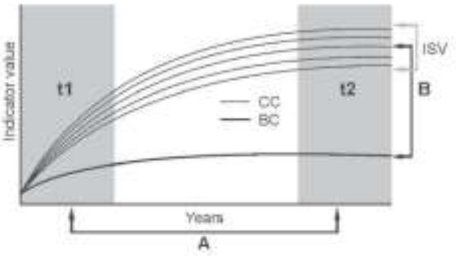

Fig. 1 Evaluation of simulated forest development indicators. Mode *A* compares the forest development indicators between two time slices of the simulation period under the baseline climate. Mode *B* compares the forest development indicators driven by the baseline climate and climate change scenarios within a single time slice. *BC* baseline climate, *CC* climate change scenario, *t1*–*t2* time periods, *ISV* inter-scenario variability

Two evaluation modes of simulation output were used (Fig. 1). Mode A compared the forest development indicators between two time slices of the simulation period under the baseline climate and described the cumulative effect of management, disturbances, and stand development. Mode B compared the forest development indicators simulated under the baseline climate and climate change scenarios within a single time slice; mode B therefore described the effect of climate change free of any other effects. The results of the simulations, which were run in 25 RSTs (Supplementary material B), were averaged and recalculated to per hectare units and were weighted according to the basal area of each species. We evaluated the response of Norway spruce, silver fir, and European beech, which are of particular interest in the CM because they form original forest communities occurring in the Carpathians.

Evaluated indicators

The used forest dynamics model transforms the driving environmental variables into suitability scores in the range of 0–1 using a set of species-specific functions. We evaluated the response of individual drivers to climate change using evaluation mode B (Fig. 1) to assess the climate change-mediated alteration of species-specific growing condition in the model region (Supplementary material F).

We addressed biomass production (BP) per species evaluated cumulatively during the investigated period. The total harvested volume, harvested timber volume, and harvested fuel and pulp wood volume are evaluated as indicators of commercial importance; these indicators are evaluated for CM-based simulations only (Supplementary material E).

Species and stand structure diversity are evaluated using the true diversity index (D) (Jost 2006), which is an indicator of tree species diversity, and the tree size diversity index (H), which aggregates the diversity of tree heights and diameters (Staudhammer and LeMay 2001). Also evaluated were the development of dead wood abundance (DWV, $m^3\ ha^{-1}$) and number of large standing dead and living trees per hectare (LSTN). All of these are recognized as indicators of habitat diversity for numerous forest-dwelling species and may respond differently to climate change and management (Lassauce et al. 2011; Larrieu and Cabanettes 2012). Additional details on the indicators are provided in Supplementary material E.

The total cumulative volume of dead trees was used to evaluate the effect of the two management systems (CM vs. NM) on forest vulnerability to disturbances. In addition, the ratio of cumulative volumes of salvage and total (salvage plus planned) cutting was evaluated for CM-based simulations.

Results

Tree growth conditions

The species-specific suitability scores of climatic driving variables used in the model Sibyla showed a specific pattern of change between the baseline climate and the mean climate projection (i.e., the average of five climate change scenarios) in the period 2071–2100 (Supplementary material C). The evaluation based on mode B (Fig. 1) showed that the growth condition of all species worsened at lower elevations, while the response at high elevations was variable; in the latter case, however, the scores remained closer to the optimum range. The scores of water availability-related variables (precipitation, soil moisture, and aridity index) decreased across the region for all species, and the decrease was the most pronounced in spruce. For spruce, beech, and fir at lower elevations, the water availability indicators reached low values even under the baseline climate and decreased further under climate change. Moreover, the projected air temperature exceeded fir- and spruce-specific limits, and the respective scores approached zero. Hence, both water scarcity and high temperature can be expected to limit tree growth at lower and medium elevations of the region.

In contrast, a slight improvement in growing conditions related to the temperature increase was projected to occur at the highest elevations, although this improvement was accompanied by a slight decrease in water availability-related indicators.

No change was projected in the case of the non-climatic variables, and they are all near the optimum range of all species. A difference in soil nutrient content between the elevation zones (EZs) relates to the occurrence of calcareous bedrock at the highest elevations of the region, while the remainder of the region contains nutrient-poorer and shallower soils (Supplementary material A).

Biomass production and harvested biomass

The combined effect of management, disturbances, and stand development (evaluation mode A, Fig. 2) showed that spruce BP declined under both management systems. While the difference was not significant in the lowest EZ, CM induced a substantial decrease in spruce BP in the rest of the region. Climate change adversely affected spruce BP (evaluation mode B) across the region under both management systems. The decline was the most pronounced with CM in the lowest and medium EZ, where BP dropped to 50 and 35 % of the baseline climate simulations, respectively. The decline with NM reached 25 and 10 %, respectively. In the highest EZ, NM and CM induced a decline of 15 and 5 %, respectively.

Beech BP constantly increased in time under both management systems and the increase was greatest in the lowest EZ with NM (evaluation mode A). The change in beech BP in the highest EZ, which is naturally dominated by conifers, was negligible. Beech BP was significantly less sensitive to climate change than spruce BP (evaluation mode B). The difference in beech BP response between the management systems was negligible except in the highest EZ, where BP increased by ca. 10 % with NM and decreased by ca. 5 % with CM. In the lowest EZ, BP decreased by up to 15 % under both management systems.

Fir BP increased under both management systems (evaluation mode A), and the increase with NM was severalfold higher than with CM. This was not the case in the lowest EZ, where the difference between the management systems was not significant. The effect of climate change was neutral-to-positive (evaluation mode B) and was generally greater with CM than with NM. In the lowest EZ, BP increased by 10 % (NM) to 25 % (CM), and in the rest of the region remained unchanged with NM and increased by up to 20 % with CM.

The total harvested volume over the entire simulation period (i.e., 2010–2100) declined by ca. 7 % (from 402 to 375 $m^3\ ha^{-1}$) in response to climate change (evaluation mode B). The harvested timber volume decreased by ca. 9 % (from 292 to 266 $m^3\ ha^{-1}$), and the harvested fuel wood decreased by ca. 1 % (from 110 to 109 $m^3\ ha^{-1}$).

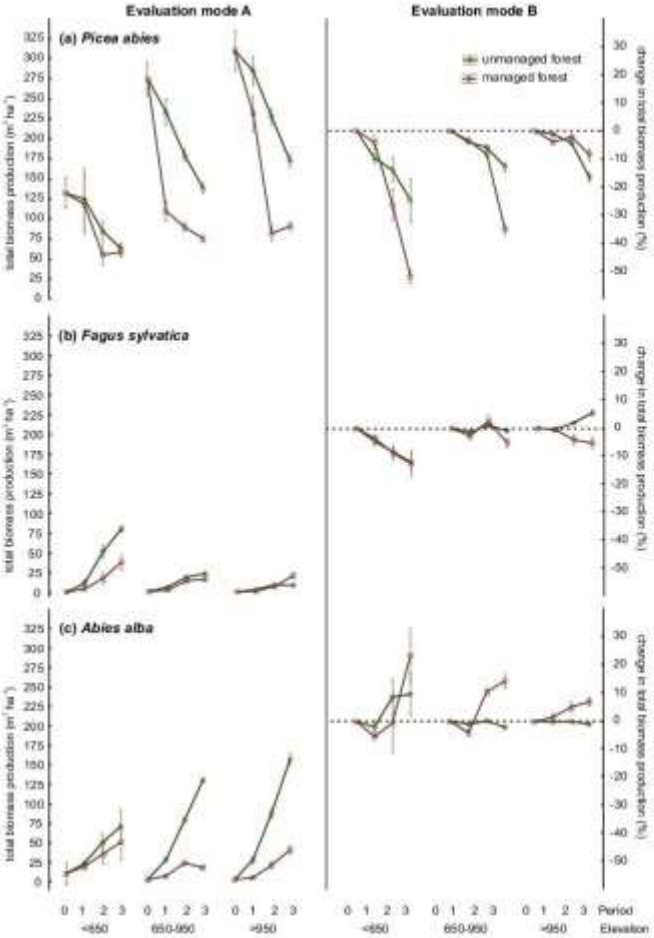

Fig. 2 Development of biomass production in three elevation zones in the Goat Backs Mts. simulated without the effect of climate change (*three left panes*), and the percentage of change between the simulations run under climate change scenarios and the baseline climate (*three right panes*). Periods: 0—2010, 1—2011–2030, 2—2031–2070, 3—2071–2100

Biodiversity indicators

Tree species diversity in terms of the true diversity index D increased during stand development across the region in response to CM and the high mortality rates of spruce (evaluation mode A). The increase was more pronounced at lower than at higher elevations, which reflects the artificial regeneration rates applied for particular sites (Supplementary material B). Simulations with NM showed an increase in D in the lowest EZ only, while it remained unchanged in the rest of the region. The tree size diversity index H increased equally in the course of stand development with both CM and NM, except in the lowest elevation zone, where NM induced greater increase than CM.

The response of D and H (evaluation mode B, Fig. 3) to climate change was different: While both indices remained unchanged in the highest EZ under both management systems, H was projected to decrease under both systems in the rest of the region. The most remarkable effect of climate change was an increase in D with CM in the lowest EZ. The response of D to climate change with NM was not significant except in the lowest EZ, where D showed a minor decrease.

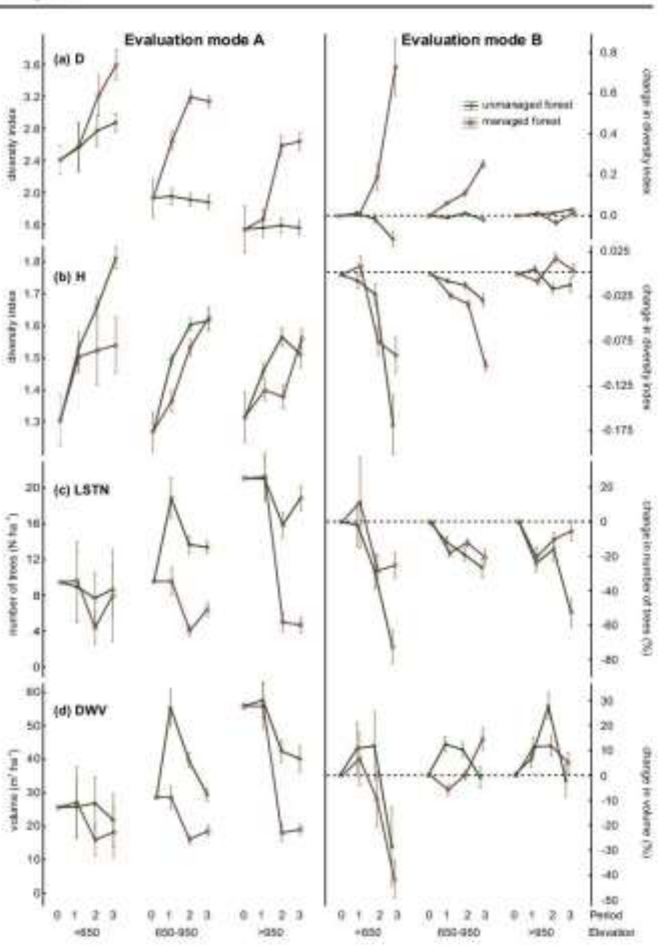

Fig. 3 Development of four biodiversity indicators in three elevation zones of the Goat Backs Mts. Index values simulated without the effect of climate change (the *three left panes*), and the difference between simulations with climate change scenarios versus the baseline climate (the *three right panes*) is presented. *D* true diversity index, *H* tree size diversity index, *LSTN* number of large standing trees per hectare, *DWV* dead wood abundance in m^3 ha^{-1}; periods: 0—2010, 1—2011–2030, 2—2031–2070, 3—2071–2100

The evaluation under the mode A showed that LSTN was significantly higher with NM than with CM, except in the lowest EZ, where the difference was not significant. The index was responsive to climate change (evaluation mode B), and LSTN decreased by the end of the simulation period by up to 80 % at the lowest elevation with NM. In the rest of the region and with CM, the response was lesser. DWV abundance was significantly higher in the medium and higher EZ with NM than with CM because CM removes dead wood instantly for sanitary reasons. Climate change reduced DWV at the lowest elevation by the end of the century by 30–40 % with insignificant difference between management systems.

Forest damage

The simulations run under the CM scenario were characterized by a high rate of salvage cutting that was almost 70 % of the total harvested volume at the beginning of the simulation period. The share of salvage cutting began to decline instantly after the simulation began and reached a steady state of ca. 56 % in 2070 (Fig. 4, evaluation mode A).

The cumulative volumes of dead trees simulated under the baseline climate significantly differed with CM versus NM (17500 vs. 24500 t ha^{-1} cumulated during the entire simulation period). Because mortality rates during the simulation period were assumed to be constant, the effect

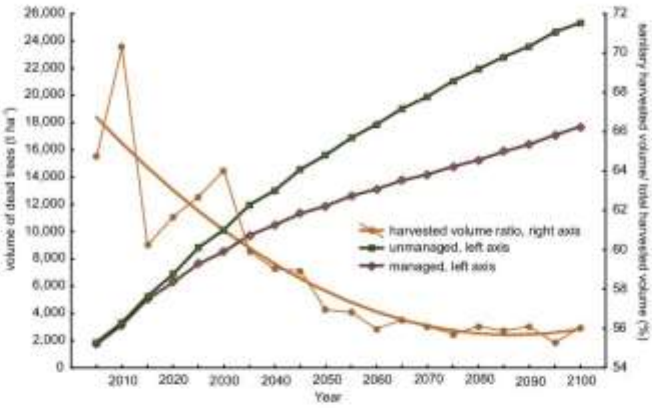

Fig. 4 Ratio of cumulative sanitary harvested volume to the total harvested volume (sanitary and planned), and cumulative volumes of dead trees simulated with the currently applied management and without management. The simulations were driven by the climate referring to the period 1961–1990

of climate change both on the salvage logging rate and on the amount of dead trees was negligible (not presented).

Discussion

This study has investigated how forest management and climate change might affect future biomass production and forest biodiversity indicators in spruce-dominated forests in the Central Western Carpathians. In the following chapters, we discuss, in the view of our research, the prospects of such forests and the sustainability of applied forest management.

Inter-species dynamics and biomass production

The change in biomass production induced by climate change showed an obvious pattern of growth decline at low elevations related to an increasing water shortage, and a minor growth acceleration at high elevations that was mainly induced by an increase in air temperature and a prolonged growing season (Walther et al. 2002; Peñuelas et al. 2007; Hlásny et al. 2011).

For spruce and beech, these responses were obvious under both management systems, although the response to CM was more pronounced for spruce than for beech. The difference between management systems might result from NM having a larger share of old trees, whose production rate may be less sensitive to climate than the younger trees that appear after management intervention and that have higher growth rates. However, findings on the age-related climatic sensitivity of trees differ among studies (e.g., Linderholm and Linderholm 2004; Mamet and Kershaw 2013). Moreover, the applied thinning from below removes trees, which growth dynamics are predominantly driven by available light resources. It follows that the aggregated stand-wise climatic sensitivity could have increased. This also suggests that the predictability of spruce forest development under climate change might be greater in unmanaged than in managed forests. These inferences are supported by the inter-climate change scenario variability of all of the evaluated indicators, i.e., the variability of these indicators was much higher with management than without management (Supplementary material G).

The climate change scenarios used in this study showed an average increase in air temperature by 3 °C and decrease in annual precipitation by 13 % by the end of the century. These changes resulted in suboptimal values of all drivers related to water availability and in a decline in simulated biomass production at lower to middle elevations in the region. This suggests an increasing importance of drought as a driver of regional forest dynamics (Lindner et al. 2010; Mátyás et al. 2010; Hlásny et al. 2014a, b, 2015).

For spruce, which is particularly sensitive to changes in soil water regime, climate change is likely to induce a decrease in species productivity and competitive capacity (Schlyter et al. 2006). Simulated spruce biomass production decreased along the elevation-climatic gradient from 50 to 10 % under the current management, but the decrease was less without management. This differential response of spruce biomass production to management can be related to the management support to non-spruce species, which perform better than spruce in a drier environment and therefore increasingly compete with spruce; without management, spruce faced less inter-species competition, and its production therefore declined less.

The effect of climate change was smaller on beech than on spruce; beech production declined from 5 to 15 %

across the region under the current management, while unmanaged development led to an increase by ca. 8 % at the highest elevations. The European beech has been broadly promoted as a suitable surrogate species in the conversion of secondary Norway spruce forests (Spiecker et al. 2004), and our results supported this. However, a growing body of evidence suggests that beech can be particularly sensitive to climate change and that a drought-induced dieback of beech may even occur (Peñuelas et al. 2007; Mátyás et al. 2010). Hence, species vitality under climate change should be cautiously evaluated.

The production of fir steadily increased during the simulation period (evaluation mode A), and this increase was further supported by climate change (evaluation mode B). Fir response differed between management systems; a positive response to climate change was observed with CM but not with NM. In contrast, fir productivity simulated without the effect of climate change (evaluation mode A) was significantly higher without management than with management. This is likely due to the shade tolerance of the species (Paluch and Jastrzebski 2013). Fir regenerates and grows better in the closed-canopy stands typical of unmanaged forests than in managed forests with strip-based harvesting applied in the study region.

At higher elevations, the temperature-related drivers approached the optimal range by the end of the century for some species, which therefore benefited from climate change. Beech in unmanaged stands and fir in managed stands showed an increase in biomass production by up to 10 %; however, fir production increased at all elevations. Although an increase in production at higher elevations does not compensate for the reduced production in the rest of the region, improved production of some species may support forest protective and regulation functions, which are particularly important in high elevation forests (Bigot et al. 2008). Spruce at high elevations did not benefit from the increased air temperature, and thus, the temperatures closer to the optimal range did not compensate for the suboptimal range of water availability-related drivers. However, a comparable simulation from the adjacent region (Hlásny et al. 2014a) predicted that an unmanaged spruce stand at 1222 m a.s.l. would increase the total amount of accumulated carbon by 13 % and net ecosystem exchange by 28 % by the end of the century. This difference between studies may be attributed to the reference climate being drier in the region of the current study with annual precipitation totals ca 20 % lower than in the region of the earlier study.

Effects on biodiversity indicators

Our findings indicate a positive combined effect of forest management and climate change on tree species diversity; this effect was amplified by a high mortality rate of dominating spruce that supported the emergence of other species. The positive response of tree species diversity to climate change was related to the effects of climate change on species competitiveness (Cavin et al. 2013; Mette et al. 2013), which showed a specific pattern along the altitudinal gradient. This suggests that co-occurring species in the future are likely to reach the so-called climatic turning point (Mette et al. 2013), which refers to the conditions under which the competitive capacity of concurrent species ranks reversal.

An increase in diversity can help stabilize regional forests by enhancing compensatory dynamics between species (Morin et al. 2014), by mitigating disturbance impacts (Pedro et al. 2014), and by increasing the inherent adaptive capacity of forests (Lindner et al. 2010). Moreover, enhanced species mixtures in spruce monocultures may increase the survival of spruce (Griess et al. 2012; Neuner et al. 2014), which is particularly important in the model region. In general, an increase in climate change-induced diversity should be considered specific to commercial, low-diversity forests, because the overall effect of climate change on biodiversity is expected to be negative (Thuiller et al. 2005, 2007).

In NM simulations, species diversity showed a minor increase only at the lowest elevations (evaluation mode A) and was almost unaffected by climate change (evaluation mode B). This suggests that commercial spruce forests, which are not actively adapted to climate change, tend to preserve their monospecific composition at a cost of substantially increased forest damage.

The abundance of dead wood and large standing trees was significantly affected by management system, and the divergence between management systems was greatest at medium and high elevations. Although such processes can enhance biodiversity (Lassauce et al. 2011), the accumulation of dead wood and over-mature trees in spruce forests with high densities of bark beetles may increase spruce mortality and harm forest functioning (Wichmann and Ravn 2001). Such a feedback, however, was not considered in the current modeling exercise.

Disturbance-related mortality

Although forest disturbance regimes are likely to be modified by climate change, we kept the rate of forest damage equal to the parameterization period 1998–2009 because of the theoretical difficulties of forecasting forest damage under climate change. Seidl et al. (2014) showed that forest damage in Europe is likely to increase in the period 2021–2030 relative to the period 1971–1980 by 229 % in the case of wind and by 764 % in the case of bark beetles. We, however, did not find the Europe-wide projection applicable in the model region, where the rate of forest disturbances has already been greatly elevated. The use of the projection by Seidl et al. (2014) would probably cause our model to predict the rapid extinction of spruce across the study region (as was suggested for some regions in Europe, for example, by Temperli et al. 2013). We argue that with regard to current management objectives, a decreasing trend in forest damage, increasing forest diversity, and a substantial investment in forest protection could result in spruce continuing to be an important component of regional forests.

Implications for management

The current management system mainly attempts to minimize forest damage while maximizing timber production and does not directly consider climate change adaptation. Current management, for example, fails to emphasize the need for increased drought resistance, which our findings indicate to be important. The importance of forest drought resistance is also indicated by the projected expansion of Mediterranean climates (Alessandri et al. 2014) and climatic envelopes of Mediterranean oaks (Hanewinkel et al. 2012) into Central Europe. Bolte et al. (2009) suggested that the establishment of so-called neonative forests, including the intermixing of native and non-native tree species and provenances, may be an option for climatically exposed sites. Such a concept, however, goes beyond the current efforts of forest conversion in Central Europe as well as the current legislation of most Central European countries.

Our finding that management and disturbances have a greater effect on regional forest dynamics than have the climate change (in terms of direct effects on tree growth, Supplementary material H) suggests that available resources should be primarily invested into disturbance management and optimized silviculture systems. The importance of disturbance management is underscored by the slow decrease in the salvage logging rate, which in our simulations continues to account for more than half of the total harvests by the end of the century (even without the amplifying effect of climate change). This agrees with Thom et al. (2013), who suggested that drivers of forest disturbance regime can be influenced by forest management but that the response times are likely to be slow.

Conclusions

Our modeling study shows how the future development of forests in Central European mountain regions may be affected by climate change, forest disturbances and management. We suggest that the presented changes in forest dynamics and competition between species should be considered by forest managers in their attempts to increase forest adaptive capacity and support the sustainability of ecosystem services provisioning.

At the same time, we show that forest management has a remarkable capacity to moderate forest damage and the adverse effects of climate change and that supporting forest diversity is of paramount importance. The projected rate of forest adaptation, however, seems insufficient to secure the sustainable provisioning of desired ecosystem services under climate change, and a broader range and greater intensity of adaptation actions is obviously needed. We emphasize the threat of increasing drought to regional forests, which has not been receiving adequate attention in Central Europe so far, even though climatic projections have consistently indicated that drought is likely to significantly increase under climate change.

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Sustainability of forest management in a Central European mountain forest: the role of climate change

SUPPLEMENTARY MATERIAL

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Supplementary material A Study region and applied forest management

The Goat Backs Mts. model region is located in northeastern Slovakia (Central Europe) in the mountain range of the Central Western Carpathians (Fig. A1). The region covers an area of 8,226 hectares with 62.4% forest cover and an altitudinal range of 650–1,555 m a.s.l. Air temperature during growing season (April–September) ranges from 12–15°C, and growing-season precipitation ranges from 380–510 mm. Cambisols and Podsols prevail, while Rendzinas occur in the calcareous bedrock at the highest elevations.

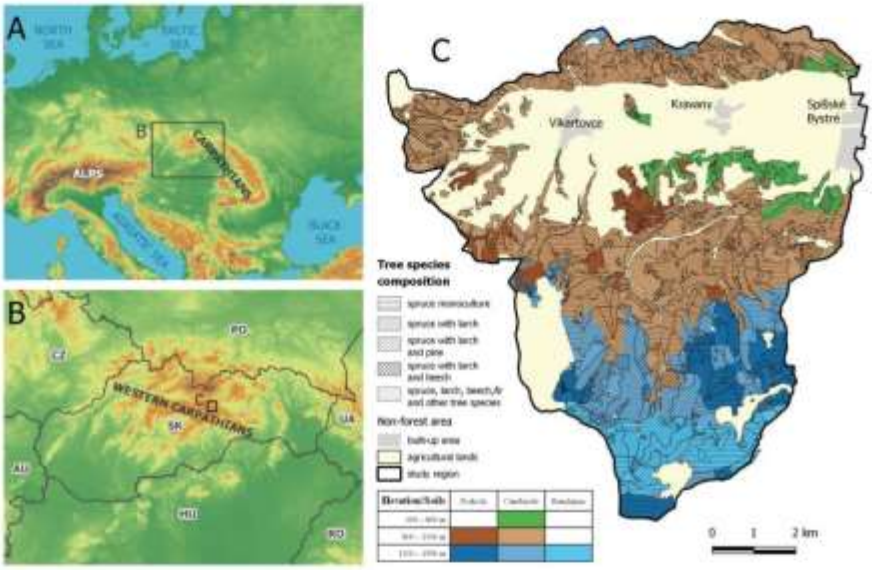
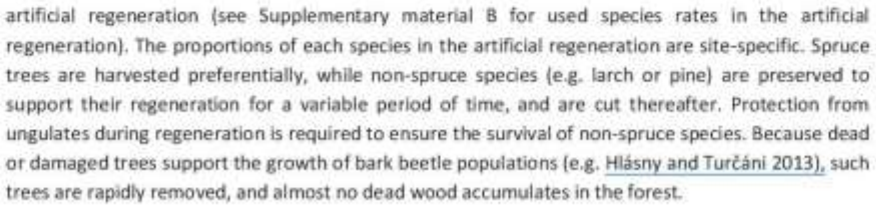


Fig. A1 Location of the Goat Backs, Mts. model region in Europe (A, B), and regional forests, main soil types, and elevation zones (C). Such parameters were used to identify forest stands representative of the study region to be used for forest development simulations.

Since 2003, the incidental felling related to wind and snow damage followed by bark beetle outbreaks has been annually approaching 100% of the total volume of harvested timber. Even-aged management with a rotation length of 95-140 years (depending on species composition and site) is applied. Tending is applied at a thicket stage to reduce stand density to the 90% of the full stocking (the full stocking for a given site is specified using growth and yield tables). Between 2 to 4 thinning operations of variable intensity are applied, depending on stand density and site index. Regeneration system is uniform shelterwood in stands with fir and/or beech admixtures. In such stands, two-phase shelterwood cut at a maximum area of 3.0 ha with 4 - 6 harvest cycles is applied. In spruce monocultures, a small-scale clearcutting system with 3 harvest cycles is applied, with a maximum clear-cut area of 3.0 ha.

Because of high amounts of sanitary felling induced by the wind and bark beetles, the forest stands are stabilized by increases in the proportion of species other than Norway spruce by means of



artificial regeneration (see Supplementary material B for used species rates in the artificial regeneration). The proportions of each species in the artificial regeneration are site-specific. Spruce trees are harvested preferentially, while non-spruce species (e.g. larch or pine) are preserved to support their regeneration for a variable period of time, and are cut thereafter. Protection from ungulates during regeneration is required to ensure the survival of non-spruce species. Because dead or damaged trees support the growth of bark beetle populations (e.g. Hlásny and Turčáni 2013), such trees are rapidly removed, and almost no dead wood accumulates in the forest.

Supplementary material B Criteria on the selection of representative stand types to be used for forest development simulations

Tab. B1 Criteria used to select the representative stand types (RSTs) for forest development simulations. Each combination of site and stand criteria is represented by a single RST, and each RST is representative of a certain part of the study region (Fig. A1). Species proportions used in the artificial regeneration in each RST are also indicated. Species codes: S – spruce, F – fir, L – larch, B – beech, M - maple

Species composition	Elevation (m a.s.l.)	Soil type	RST ID	Area (%)*	Regeneration (%)
Spruce	600-800	Cambisols	1	0.38	S 50, F 10, P 10, L10, B 10, M 10
	801-1100	Cambisols	2	10.79	S 30, F 20, L 10, B 30, M 10
		Podsols	3	0.87	S 40, F 20, L 20, B 20
	1101-1500	Cambisols	4	4.42	S 40, F 20, L 20, B 20
		Podsols	5	4.92	S 60, F 20, L 10, B 10
		Rendzinas	6	4.19	S 30, F 10, P 20, L 10, B 30
Spruce with larch	600-800	Cambisols	7	1.86	S 50, F 10, P 10, L10, B 10, M 10
	801-1100	Cambisols	8	15.84	S 50, F 10, P 10, L10, B 10, M 10
		Podsols	9	2.53	S 40, F 20, L 20, B 20
	1101-1500	Cambisols	10	7.32	S 60, F 20, L 10, B 10
		Podsols	11	1.96	S 60, F 20, L 10, B 10
		Rendzinas	12	3.86	S 20, F 20, B 30, M 30
Spruce with larch and pine	600-800	Cambisols	13	1.21	S 30, F 20, L 10, B 30, M 10
	801-1100	Cambisols	14	7.20	S 50, F 10, P 10, L10, B 10, M 10
		Podsols	15	0.20	S 50, F 10, P 10, L10, B 10, M 10
Spruce with larch, beech and fir	600-800	Cambisols	16	0.38	S 50, F 10, P 10, L10, B 10, M 10
	801-1100	Cambisols	17	5.69	S 40, F 20, L 20, B 20
		Podsols	18	1.21	S 60, F 20, L 10, B 10
	1101-1500	Cambisols	19	1.12	S 60, F 20, L 10, B 10
		Rendzinas	20	0.19	S 20, F 20, B 30, M 30
Mixture of spruce, larch, pine, fir, beech and maple	600-800	Cambisols	21	1.84	S 30, F 20, L 10, B 30, M 10
	801-1100	Cambisols	22	15.52	S 50, F 10, P 10, L10, B 10, M 10
	1101-1500	Cambisols	23	3.18	S 30, F 20, L 10, B 30, M 10
		Podsols	24	2.20	S 60, F 20, L 10, B 10
		Rendzinas	25	1.11	S 20, F 20, B 30, M 30

*per cent of the study region

Supplementary material C Description of climate change scenarios and of the baseline climate used to drive the forest development simulations

Tab. C1 Future climate statistics refer to the period 2071–2100. Although the data refer to elevation 1,000 m a.s.l., the projected change in air temperature and precipitation is almost uniform across the region. Model coding (c1–c5) follows the magnitude of Δ(°C) in the period 2071–2100. Abbreviations: MAT – Mean annual air temperature; PVS – Precipitation during vegetation season; Δ – Change between a scenario and the baseline climate

Scenario ID	RCM	Driving GCM	MAT (°C)	MAT Δ(°C)	PVS (mm)	PVS Δ (%)
baseline	—	—	7.0	0.0	451.0	0.0
c1	DMI-HIRHAM5	BCM	9.0	1.9	495.5	9.9
c2	DMI-HIRHAM5	ARPEGE	9.2	2.2	294.2	-34.8
c3	ICTP-RegCM	ECHAM5-r3	9.8	2.8	432.0	-4.2
c4	SMHI-RCA	ECHAM5-r3	10.3	3.2	381.0	-15.5
c5	HC-HadRM3	HadCM3Q16	11.9	4.9	351.2	-22.1
—	Average c1-c5	—	9.5	3.0	400.8	-13.4
—	St. dev. c1-c5	—	1.5	1.0	66.7	15.3

Supplementary material D Implementation of tree species-specific mortality rates in the forest dynamics model Sibyla

The records on forest damages in Slovakia (Source: National Forest Centre, internal data) in terms of volume of salvage harvests were used to calculate the mortality rates specific to a tree species and age class. The parameterisation data cover the period 1998-2009, and are based on randomly selected forest management units representing 59% of the forested area (1.14 mil. ha) and 60% of the growing stocks (273.8 mil. m^3) in Slovakia. Although particular damage agents are specified in the source data, we used the aggregated mortality rates. The total harvested volume of dead or damaged trees relative to the total volume of a given species and age class represents the mortality rate used in the simulations. Hence, the presented mortality rates include both natural tree mortality and mortality induced by disturbances.

Although the source data relate to a stand scale, we implemented the mortality rates in the Sibyla model so as each tree and age class in a stand receives a specific mortality rate. Although such a use violates the natural stand dynamics, it provides a realistic output when the data are spatially aggregated or simulation plots are representative of larger areas, as is the case of the current study.

As can be seen in Fig. D1, the mortality rates of spruce, larch, beech and oak are increasing with age, while pine and fir show the highest mortality rates at early ages. The latter fact is related to the frequent damages by snow and ice to pine, and by game to fir; the competition also increases the mortality rates for young developmental stages. The decrease in mortality rates at ages above ca 120 years is due to the fact that oldest stands in the parameterisation data are located in protected and protective forests with lower rate of damage as compared with commercial forests. However, trees older than 120 years occur in the study region only marginally.

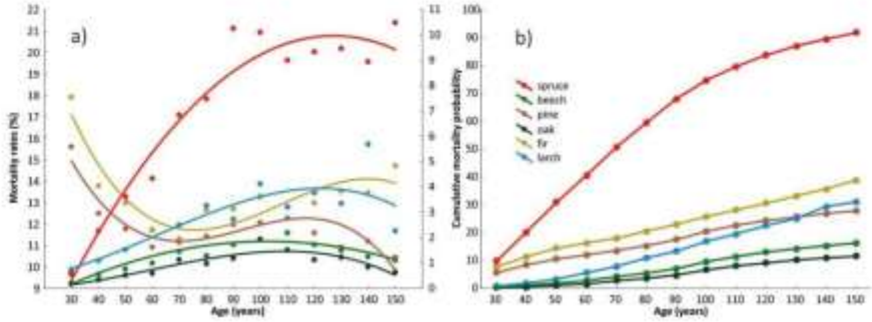


Fig. D1 Mortality rates of main tree species used in forest development simulations in the Goat Backs Mts. model region. The values represent the probability a stand is destroyed in a certain age (pane a) or up to a certain age (pane b). In the pane a, the left y-axis relates to spruce mortality rates, while the right y-axis relates to the remaining species

Supplementary material E Definition of forest development indicators addressed in the current study

Biomass production per species (BP) ($m^3\,ha^{-1}\,yr^{-1}$) includes roots, trunk, stem, branches, and leaves in both dead and living trees, harvested or not.

Total harvested biomass volume (TVH) ($m^3\,ha^{-1}\,yr^{-1}$) contains all biomass extracted during silviculture and harvesting operations

Harvested timber volume (HTV) ($m^3\,ha^{-1}\,yr^{-1}$) contains part of TVH classified on the basis of Slovak assortment tables as timber wood assortments (Petráš et al. 1996)

Fuel and pulp wood volume (HFV) contains part of TVH classified on the basis of Slovak assortment tables as fuel and pulp wood assortments

Tree species diversity was evaluated using the true diversity index D (Jost 2006), which is the exponential form of Shannon`s diversity index S:

$$\begin{cases} S = -\sum_{i=1}^{N} p_i \ln(p_i) \\ p_i = \frac{d_i}{G} \end{cases}$$

where N is the number of species, d_i the basal area of species i (m^2; in this study calculated using the basal area of tree species with diameter ≥ 5cm) and

$$G = \sum_{j=1}^{S} g_j(\mathrm{m}^2)$$

Hence the true diversity index D is defined as:

$$D = exp(H)$$

Tree size diversity index H was evaluated based on post-hoc index presented by Staudhammer and LeMay 2001:

$$\begin{cases} H_{size} = \frac{H_{DBH} + H_H}{2} \\ H_{DBH} = -\sum_{i=1}^{N_{DBH}} \frac{g_i}{G} \ln\left(\frac{g_i}{G}\right) \\ H_H = -\sum_{i=1}^{N_H} \frac{g_i}{G} \ln\left(\frac{g_i}{G}\right) \end{cases}$$

where N_{DBH} and N_H is the number of DBH and height classes present in stand, g_i the basal area (m^2) of DBH or height class i and G the basal area of stand (m^2). For DBH, we use 5 cm classes, and for height 2 m classes (Cordonnier et al. 2013).

Dead wood volume (DWV) ($m^3\,ha^{-1}$) includes standing dead trees with DBH >5 cm and lying dead wood originating from trees with DBH >5 cm at any decomposition stage.

Number of large standing dead and living trees (n ha^{-1}) (LSTN) contains all large dead and living trees with a DBH above 70 cm for conifers and above 50 cm for broadleaves. Annual probability of dead tree downing was specified in Cordonnier et al. (2013), and LSTN was modified accordingly.

Supplementary material F Climate change effect on driving variables in the Sibyla model in the Goat Backs Mts. model region

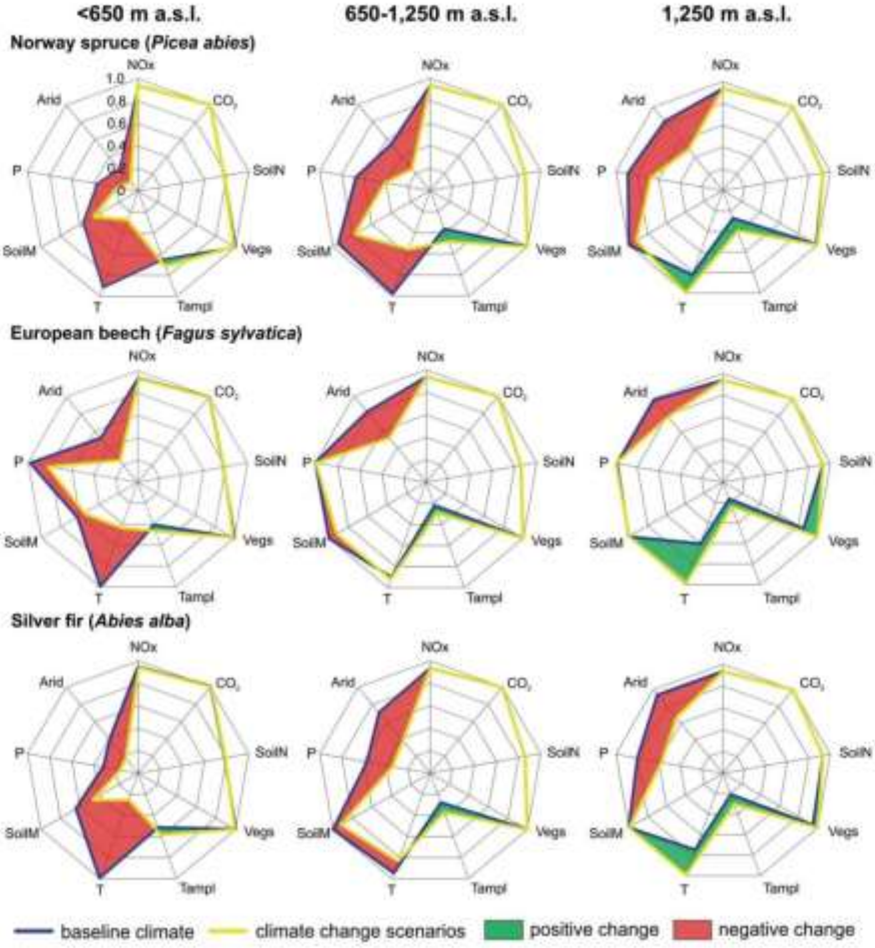


Fig. F1 Climate change induced changes in the suitability scores of environmental variables driving the forest development in the used forest dynamics model Sibyla. The scores are calculated by transformation of original variables using the tree-species specific functions. The difference in suitability score between the period 2071-2100 and the baseline climate corresponding with the period 1961-1990 are presented. The future climate is represented by the average of 5 climate change scenarios described in the Supplementary material C. Red zones represent the decrease of respective suitability score and deterioration of growing conditions, while green zones represent an improvement in growing conditions

Supplementary material G Inter-climate change scenario variability of evaluated forest development indicators

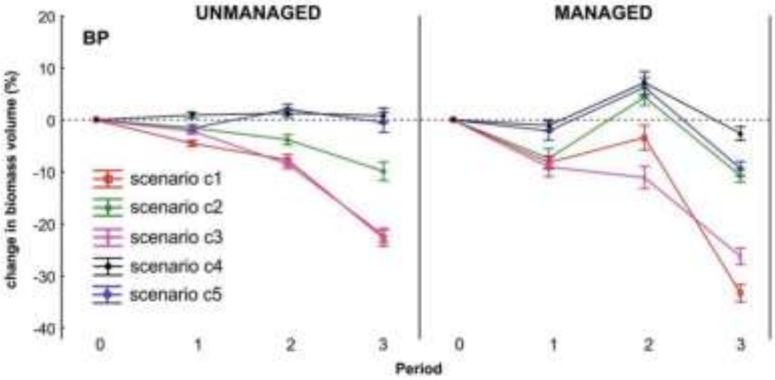


Fig. G1 Inter-climate change scenario variability of simulated total biomass production (BP). The per cent change between five climate change scenarios and the baseline climate are presented for the current management regime (right pane) and the no management regime (left pane). Description of used climate change scenarios is given in Supplementary material C. Periods: 0 – 2010, 1 – 2011–2030, 2 – 2031–2070, 3 – 2071–2100

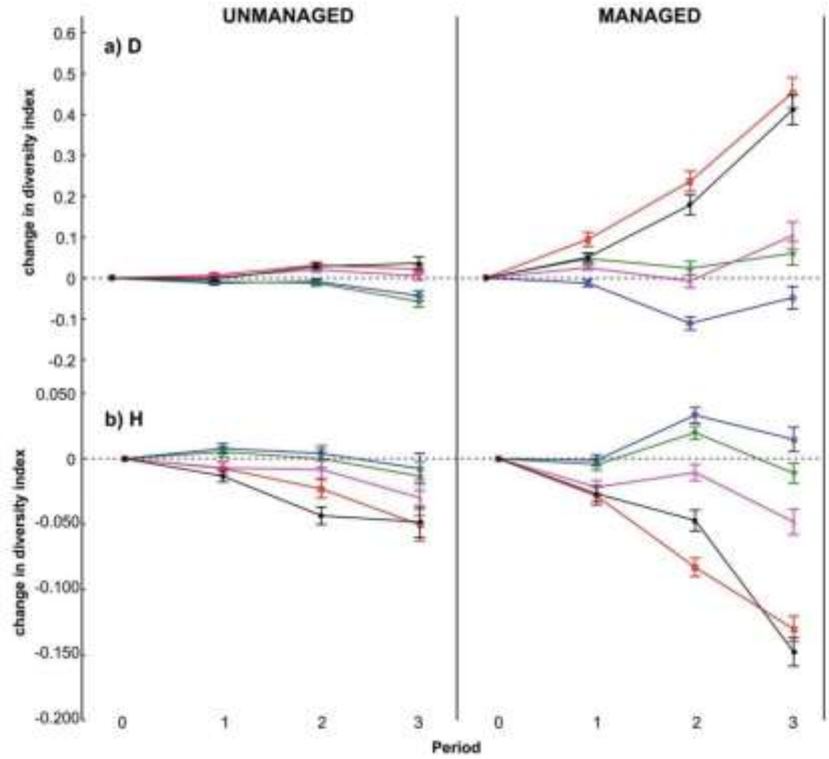


Fig. G2 Inter-climate change scenario variability of true diversity index (D) and tree size diversity index (H). The difference between five climate change scenarios and the baseline climate is presented for the current management regime (right pane) and the no management regime (left pane). Periods: 0 – 2010, 1 – 2011–2030, 2 – 2031–2070, 3 – 2071–2100

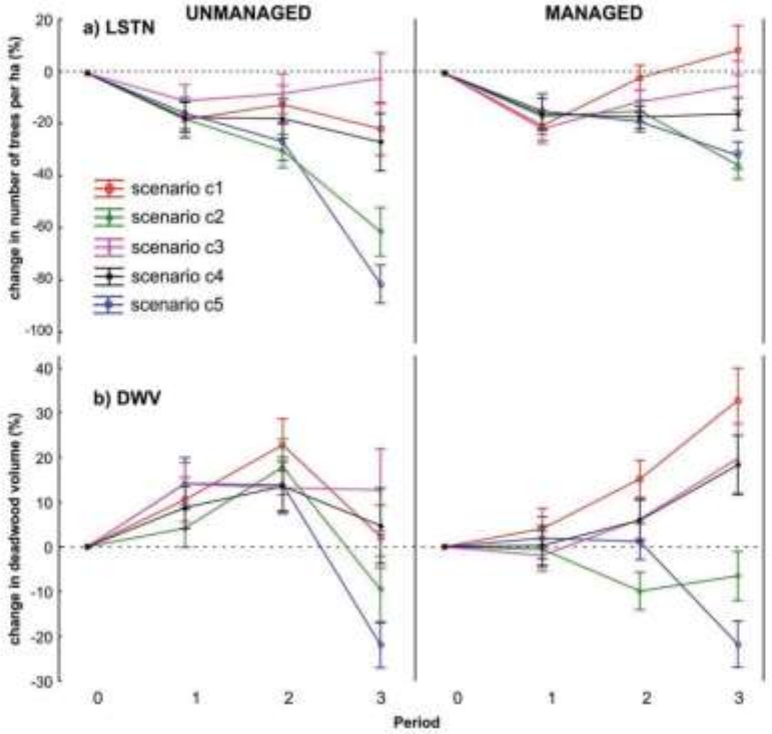


Fig. G3 Inter-climate change scenario variability of simulated of number of large standing trees per hectare (LSTN) and dead wood abundance in m^3 ha^{-1} (DWV). The per cent change between five climate change scenarios and the baseline climate is presented for the current management regime (right pane) and no management regime (left pane). Periods: 0 – 2010, 1 – 2011–2030, 2 – 2031–2070, 3 – 2071–2100

The inter-climate change scenario variability of the total BP (i.e. that of all species in the region) under the CM scenario ranged from 0 to -35% of the baseline-climate simulations; the greatest decrease was with c5, the warmest scenario (Tab. C1). The variability with NM ranged from 0 to -20% of the baseline-climate simulations; the greatest decrease was with scenario c5 and with c2, the driest scenario (Tab. C1).

The inter-climate change scenario variability of differences between the climate change- and baseline climate-driven simulations of both D and H was much higher with CM than with NM (Fig. G2). The changes ranged from a minor decrease to a significant increase in D, and from a minor increase to significant decrease in H. LSTN showed larger variability with NM than with CM, and range from 0 to -80% of the baseline climate simulations. The inter-climate change scenario variability of DWV was higher with CM (ca. -20 – 30 %) than with NM (ca. ±20 %).

Supplementary material H Relative importance of main forest development drivers

Because forest development in the region is predominantly driven by forest disturbances and management, and potentially by climate change, we determined the proportion of variability in simulated values accounted for by these drivers. We used a factorial analysis of variance with higher-order interactions based on the generalized linear model (GLM) to evaluate the relative effect of these factors (for more details, see Hlásny et al. 2014). To facilitate such evaluation, the simulations were run not only with CM and NM but also under a disturbance-free scenario (results of these simulations are not presented in this study). Hence, the statistical design had the following structure: the Management factor contained the levels "no management" and "current management", and the Disturbances factor contained the levels "disturbances-yes" and "disturbances-no". The Climate factor contained levels "no-climate change" and "climate change"; the latter level contained the simulations run under the five climate change scenarios (Tab. C1). The analysis was conducted in Statistica v. 12 (StatSoft Inc.).

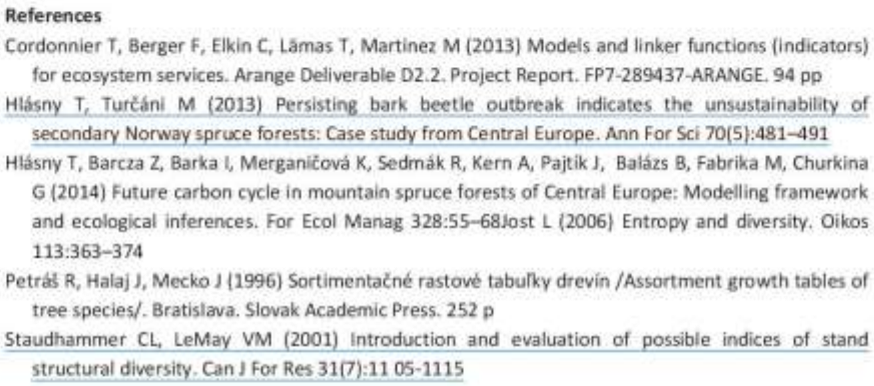
The quality of GLM fit to the evaluated indicators as indicated by R^2 values was variable, which limits some of our interpretations (Tab. H1). The results show that D is mainly driven by forest management (39% of the total variability), and this agrees with the significant difference in D simulated under the two management systems (Fig. 3 in the article); the remaining portion of the total variability was not captured by the GLM. The relative effects on H and DW cannot be evaluated because of low R^2 values (0.01 and 0.18, respectively). DWV, however, was significantly affected ($p < 0.001$) by management and disturbances. LSTN was well fit by the model ($R^2 = 0.75$), and management, disturbances, and their interaction accounted for 39, 22, and 14% of the total variability, respectively.

The model fit for TBP was also very good ($R^2 = 0.72$), and management, disturbances, and their interaction accounted for 30, 26, and 15% of the total variability, respectively. For TVH ($R^2 = 0.36$), management, disturbances, and their interaction accounted for 22, 7, and 8% of the total variability.

The relative effect of climate change was insignificant for all variables, even though the results are based on the period 2070-2100, when the divergence among the five climate-change scenarios used was high (Supplementary material C).

Tab. H1 The percentages of the total variability in stand development indicators attributed to the main forest development drivers. The data refer to the period 2071-2100. The underscored values are statistically significant at $p<0.001$. Abbreviations: Clim – climate change, Man – management, Dist – disturbances, × – interactions, H – tree size diversity index, D – true diversity index, DWV – dead wood volume, LSTV – large standing tree volume, BP – total biomass production, TVH – total harvested volume

Forest development indicators	**Forest development drivers**							
	R^2	Clim	Man	Dist	Clim x Man	Clim x Dist	Man × Dist	Clim × Man x Dist
D	0.4	0	0.39	0	0	0	0	0
H	0.01	0.01	0	0.01	0	0	0	0
DWV	0.18	0	0.13	0.05	0	0	0	0
LSTV	0.75	0	0.39	0.22	0	0	0.14	0
TBP	0.72	0.01	0.3	0.26	0	0	0.15	0
TVH	0.36	0	0.22	0.07	0	0	0.08	0



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5.6 Effect of different tree mortality patterns on stand development in the forest model SIBYLA.

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Effect of different tree mortality patterns on stand development in the forest model SIBYLA

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Abstract
Forest mortality critically affects stand structure and the quality of ecosystem services provided by forests. Spruce bark beetle (*Ips typographus*) generates rather complex infestation and mortality patterns, and implementation of such patterns in forest models is challenging. We present here the procedure, which allows to simulate the bark beetle-related tree mortality in the forest dynamics model Sibyla. We explored how sensitive various production and stand structure indicators are to tree mortality patterns, which can be generated by bark beetles. We compared the simulation outputs for three unmanaged forest stands with 40, 70 and 100% proportion of spruce as affected by the disturbance-related mortality that occurred in a random pattern and in a patchy pattern. The used tree species and age class-specific mortality rates were derived from the disturbance-related mortality records from Slovakia. The proposed algorithm was developed in the SQLite using the Python language, and the algorithm allowed us to define the degree of spatial clustering of dead trees ranging from a random distribution to a completely clustered distribution; a number of trees that died in either mode is set to remain equal. We found significant differences between the long-term developments of the three investigated forest stands, but we found very little effect of the tested mortality modes on stand increment, tree species composition and diversity, and tree size diversity. Hence, our hypothesis that the different pattern of dead trees emergence should affect the competitive interactions between trees and regeneration, and thus affect selected productivity and stand structure indicators was not confirmed.

Key words: *Ips typographus*; dispersal pattern; empirical forest modelling; tree mortality

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1. Introduction

Models of forest dynamics have become important tools that supported forest management and increased our understanding of forest development under diverse management and natural conditions. Because forest damage is among the most important drivers of forest development with effect on the quality of ecosystems services provided by forests (Thom & Seidl 2015; Thom et al. 2016), a great deal of attention has been paid to the implementation of forest mortality processes into models (Pietsch & Hasenauer 2006; Merganičová & Merganič 2014; Seidl & Rammer 2016). At the same time, models were found highly sensitive to the mortality assumptions adopted (Bircher et al. 2015; Hlásny et al. 2014), which highlights the importance of proper implementation of algorithms driving the mortality-related processes. Despite these efforts and increasing complexity of models, Keane et al. (2001) and Bircher et al. (2015) argue that mortality algorithms implemented in models are generally based on simple assumptions and insufficient data.

Bark beetles of the genus *Ips*, and particularly the spruce bark beetle *Ips typographus* (L., 1758) (Curculionidae: Scolytinae), are the most damaging biotic agents in central European forest (e.g. Berec et al. 2013). Bark beetle-related tree mortality is a highly complex process that is driven by both the host susceptibility, bark beetle population size and diverse environmental perturbations (Wermelinger 2004; Hlásny & Turčáni 2013). Interactions between the host tree distribution, tree susceptibility and density-dependent bark beetle dispersal capacity, generate specific patterns of infested trees. Such patterns might range from the scattered occurrence of infested trees, which is typical of small beetle densities, to patchy and even a large scale infestations that typically occur when the populations are in the outbreak phase (Hlásny & Turčáni 2013). Because tree mortality patterns might affect stand structure and the quality of ecosystem services in the period following the infestation, it is desired to include such information into forest models, which operate at a scale of trees.

Among such models, the forest model Sibyla (Fabrika & Ďurský 2005) has received an increased recognition in recent years (e.g. Vacek et al. 2013; Hlásny et al. 2011, 2014, 2016; Ambrož et al. 2015; Härtl et al. 2016). The model simulates mortality at a scale of trees and considers both the inherent tree mortality (Ďurský et al. 1996, 1997) and mortality related to disturbances (Fabrika & Vaculčiak 2009). Particularly the disturbance-related mortality shows significant differences between tree species, depending on tree species vulnerability to various disturbances. Hlásny et al. (2016) developed an application that simulates the disturbance-related mortality in the model Sibyla based on the species and age-specific mortality rates derived from the 10-year records on forest damage in Slovakia; this is the algorithm we use and evaluate in this study.

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Because the used mortality rates contain the cumulative effect of all damage agents (biotic and abiotic), each of them generating a specific pattern of tree mortality, the preference of any specific tree mortality pattern might be irrelevant. However, such an approach might generate biased outputs for regions, where mortality with patchy pattern, such as that related to bark beetle infestation, prevails. It is, however, not clear whether and how the consideration of such a mortality pattern might affect stand development in the period following the infestation.

To shed a light on this issue, we present a modelling exercise that evaluates in several virtual Norway spruce-dominated stands how biomass production, tree species and stand structure diversity can develop under the random and clustered mortality modes. We hypothesize that the appearance of clearings in response to the clustered emergence of dead trees could induce regeneration processes different from those induced by the random emergence of dead trees, and thus, in the long-run, affect tree species composition of the stands. Further, we hypothesize that the different patterns of dead tree emergence will affect the competition between trees and tree increment, and that such a difference will be translated from the tree scale to the stand scale. Finally, we hypothesize that mainly stand structure diversity will be affected by the tested mortality modes, while effect on biomass production will be less pronounced. Such a research is intended to contribute to mortality parameterization in tree-based forest models and to improve the reliability of forest development simulations.

2. Data and methods

2.1. Used model and simulation design

We used here the forest model Sibyla developed by Fabrika & Ďurský (2005) (available at http://sibyla.tuzvo.sk) and repeatedly used for research, for example, by Hlásny et al. (2011, 2014, 2016), Härtl et al. (2016) and others. Sibyla is empirical single-tree oriented climate sensitive forest model with a one-year simulation step, and the core components of the model are based on the Silva model (Pretzsch et al. 2002). A detailed description of the model can be found in the studies we referred to earlier.

We used three virtual forest stands with identical site conditions to secure the comparability of simulation outputs (Table 1). The used stand parameters represent the conditions in which spruce typically grows in Slovakia. The three stands were with a different share of Norway spruce (*Picea abies* L. Karst.). (Stand code: S100 – 100%; S70 – 70%; and S40 – 40%) and with a different admixture of other species (Table 2). The admixed species were European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Scots pine (*Pinus sylvestris* L.).

The inherent tree mortality (i.e. mortality related to competition) is implemented according to Ďurský et al. (1996) and Ďurský (1997). The disturbance module that is inherently implemented in the model (Fabrika & Vaculčiak 2006) was not used in this study, and we used an external module developed by Hlásny et al. (2016) instead. The latter module was developed in the Python and SQL languages, and the module allows flexible adjustments of a number of mortality settings. The disturbance mortality rates used here were specific to tree species and age class, and were parameterized based on the forest disturbance records for the period 1998–2009 using the data from the whole of Slovakia (Hlásny et al. 2016) (Table 3).

Table 1. Stand and site condition of the three simulated forest stands.

Stand and site parameters	Value
Elevation [m a.s.l.]	982
Soil type	Cambisol
Stand density	0.95
Initial age [years]	40
Mean air temperature during vegetation season [°C]	12.5
Precipitation totals during vegetation season [mm]	727

Table 2. Types of tree species composition in the three simulated forest stands.

Stand / species proportion [%]	Spruce	Fir	Beech	Pine
S100	100	0	0	0
S70	70	15	15	0
S40	40	25	25	10

Such initial rates were modified to consider the reduced susceptibility to infestation for stands with the admixture of non-spruce species based on Griess et al. (2012). The correction accounted for 3% for stands with spruce up to 80% and 15% with spruce below 60%.

Development of each stand was evaluated during a 200-year period, because the divergence of the tested stand development indicator is likely to occur in longer runs only. The simulations were run with the natural regeneration module activated (Merganič & Fabrika 2011). No management operations except for the removal of dead trees were applied. Each simulation was run ten-times to consider the variability related to the differences in the initial tree positions and stochasticity related to tree mortality and other model parameters.

Table 3. Tree species- and age class-specific mortality rates used to drive the forest mortality in the current study.

	Tree species- and age class-specific mortality rates					
	Spruce proportion in a stand [%]			Beech	Fir	Pine
Age class	>80	60–80	<60			
<30	0.10	0.10	0.08	0.01	0.08	0.05
31–40	0.11	0.11	0.10	0.01	0.05	0.04
41–50	0.13	0.12	0.11	0.01	0.03	0.02
51–60	0.15	0.14	0.13	0.01	0.03	0.02
61–70	0.16	0.16	0.14	0.01	0.02	0.02
71–80	0.19	0.18	0.16	0.01	0.03	0.02
81–90	0.20	0.19	0.17	0.02	0.03	0.03
91–100	0.20	0.20	0.17	0.02	0.03	0.03
101–110	0.20	0.19	0.17	0.02	0.03	0.03
111–120	0.20	0.19	0.17	0.02	0.03	0.02
121–130	0.20	0.19	0.17	0.01	0.04	0.02
131–140	0.21	0.20	0.18	0.01	0.04	0.02
141–150	0.20	0.19	0.17	0.01	0.04	0.01
>150	0.17	0.16	0.14	0.01	0.03	0.00

2.2. Tested mortality patterns

Two mortality set-ups were tested – a random occurrence of dead trees driven by species- and age class-specific mortality only (Table 3, mode RAN) and a clustered occurrence of dead trees (mode CLUST), where mortality is also driven by the proximity of an evaluated tree to the trees that died in the previous period. Hence, the CLUST mode generates the dead trees in a patchy pattern typical of bark beetle infestation in the epidemic phase.

In case for the RAN mode, a specific mortality rate from Table 3 is assigned to each tree in a stand based on the species and age class. Then, a real number in the 0 – 1 interval with the uniform distribution is generated for each tree to specify a threshold to which a mortality rate is compared. In case the threshold is exceeded a tree survives, otherwise a tree dies. Such a procedure is applied with a 10-year step.

In case for the CLUST mode, the procedure described above is modified based on the proximity of each tree to the trees which had died in the former simulation step. The literature review indicated that under high beetle densities (epidemic phase) most of beetles disperse over short distances (up to 100 m), and the dispersal (or the appearance of new infestation spots) disappears within 500 – 1,000 m from old infestations (Wichman & Ravn 2001; Kautz et al. 2011; Hlásny & Turčáni 2013; Stadelmann et al. 2014). Therefore, we modified the RUN algorithms so as we define the affinity of the newly infested trees to the trees infested in the previous period. The affinity with magnitude 1 causes that all new infestations might occur in trees adjacent to the old infestations, and the age effect does not apply in this case; however, the age threshold of 50 years is applied to avoid the infestation of trees, which are very unlikely to be infested. The 50-year age limit was applied though spruce bark beetle is thought to infest trees older than 70 years (Wermelinger 2004), but much younger stands have been recently found to be infested, for example, in the Czech Republic (J. Holuša, pers. comm.).

The affinity with the magnitude of 0 indicates no clustering effects and CLUST is equal to RUN. The transient affinity values can be applied to model various bark beetle dispersal patterns. The algorithm was developed in the SQLite using the Python language.

2.3. Evaluated stand development indicators

We evaluated effect of the two mortality setting on several production and stand diversity indicators. We evaluated the effect on volume increment of a stand (m^3 ha^{-1} year^{-1}); species-specific relative standing volume (% of the total stand volume), which is indicative of tree species composition; volume of dead wood (m^3); tree species and tree size diversity. The true diversity index (Jost 2006), which is the exponential form of the Shannon's diversity index, is used as the indicator of tree species diversity; species-specific basal area is used as a weight. Tree size diversity index (H), which aggregates the diversity of tree heights and diameters (Staudhammer & LeMay 2001), is used as the indicator of stand structure diversity.

3. Results

3.1. Volume increment

Different species compositions and related mortality rates caused the mean stand volume increment (m^3 ha^{-1} year^{-1}) to differ significantly between the simulated stands. While in S40 the increment culminated at ca 90th year of the simulation (stand age 130) at 27 m^3 ha^{-1} year^{-1}, the increment was steadily declining during the whole simulation period in the two remaining stands (S70 and S100). Such a decline was primarily related to the progressive mortality of the dominating spruce trees, while such an effect was less pronounced in S40 and S70.

Although we assumed that the two tested mortality modes will affect the stand density differently, and this effect will result in a differential response of stand increment, our simulations showed almost no difference between the RUN and CLUST mortality modes during the whole simulation period; minor deviations of the two curves in Fig. 1 were in the range of the respective error bars.

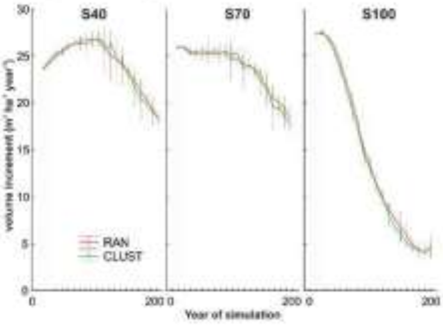

Fig. 1. Development of mean stand volume increment simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees in three forests stands. Stand codes are explained in Table 2. The error bars show the 95% interval calculated based on 10 repeated simulation runs.

3.2. Relative standing volume

Relative standing volume was investigated as an indicator of the change in tree species composition. The simulations shows that fir was performing best and its volume was steadily growing during the simulation period (Fig. 2). The decrease of spruce was related to high mortality rates, while the decrease of beech was related to the unfavorable condition for beech growth in the elevation of 1,000 m a.s.l., where beech production and ability to compete with other species were not sufficient to persist.

As in the case of mean stand volume increment, the two tested mortality modes did not affect the per-species volume significantly during the whole simulation period.

3.3. Dead wood volume

Dead wood volume generated for each year of the simulation period directly reflects the species- and age-class specific mortality rates indicated in Table 3. Development of dead wood volume in all three stands shows the presence of damage culmination phase, where the proportion of spruce and/or other overmatured trees reached maximum (Fig. 3). In S40 the damage culmination occurred ca in year 70 of the simulation period, and then the damage decrease because

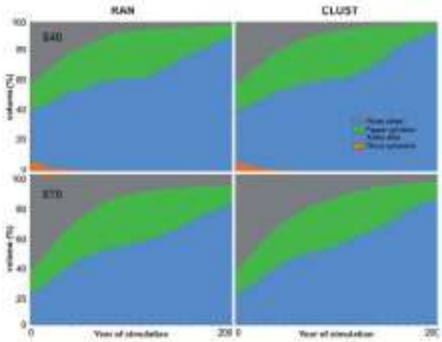

Fig. 2. Species specific standing volume calculated as the per cent of the total standing volume simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees. Stand codes are explained in Table 2. Stand S100 was not presented because of the persisting dominance of spruce.

of the increase abundance of younger and less vulnerable spruce trees. In S40 and S70 the damage peaked in ca year 170 of the simulation period, though the peak in S40 was not as sharp as in the previous stands.

Because of the stochasticity in the algorithm, which is applied to evaluate whether or not a tree dies, the inter-simulation variability is largest of the all investigated indicators. As in the previous indicators, there was no difference between the RAN and CLUST modes. In case of this indicator, however, such an output could have been expected, because the used algorithm was designated so as it affects the distribution of dead trees in a stand, while the total number of dead trees remains equal.

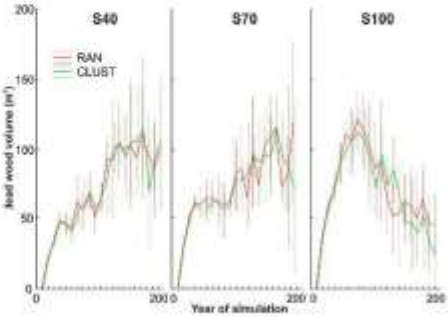

Fig. 3. Dead wood volume simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees. Stand codes are explained in Table 2.

3.4. Tree species and tree size diversity

Tree species diversity was evaluated for stands S40 and S70 but not for S100, where only spruce could regenerate and thus the stand remained monospecific during the whole of the simulation period. In S40 the initial value of the used diversity index was significantly higher than in S70 because of more equal proportions of tree species (Fig. 4). The diversity, however, sharply decreased as fir become to dominate in the stand.

Tree size diversity was increasing in all simulated stands, though the increase was rather erratic in S40. The increase was related to the occurrence of large overmatured trees, which have not died despite their high mortality rates (Table 1), as well as to the occurence of smaller trees appearing in the new generation of the forest.

Tree species diversity shows minor differences between the development driven by CLUST and RAN mortality modes, the differences are, however, in the range of the variability related to the ten simulation runs. The difference between the mortality modes as well as the inter-run variability of the tree size diversity significantly increased after ca 150 year of simulation in S40, such a pattern, however, lacks interpretation.

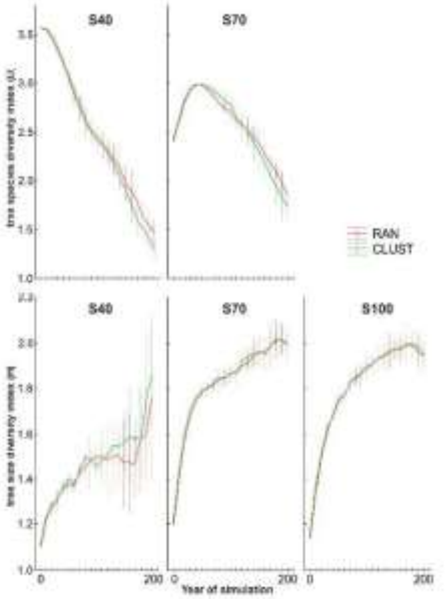

Fig. 4. Tree species (D) and tree size diversity index (H) simulated with the random (RAN) and clustered (CLUST) occurrence of dead trees. Stand codes are explained in Table 2.

4. Discussion

The model Sibyla represents a well-established forest model, which has been repeatedly used in the research of forest development driven by various management types, disturbances or by climate change (Hlásny et al. 2011, 2014, 2016; Vacek et al. 2013; Ambrož et al. 2015; Härtl et al. 2016). That the model operates at a scale of trees facilitated analyses that utilize tree positions, including the assessment of stand structure indicators or change in tree species composition. Still, there are limits in the understanding of model`s behavior, which should be explored to use the model more efficiently and support the proper interpretations of simulation outputs. We explored here how the spatially clustered occurrence of dead trees, which generates mortality patterns similar to those generated by spruce bark beetle, might affect selected stand structure and productivity indicators. Such a research might inform whether it is worth to consider the spatial distribution of dead trees in tree-based forest models, and how the selected indicators are sensitive to differences in the pattern of dead trees emergence.

We focused on three forest stands with different percentage of Norway spruce, which typically occur in central Europe. We found significant differences between the long-term developments of the three investigated forest stands, but we found very little effect of the tested mortality modes on stand increment, tree species composition and diversity, and tree size diversity. This was despite the pattern of dead trees distribution and the overall stand structure was rather different between the simulations driven by the two mortality modes (Appendix A). Hence, our hypothesis that the different pattern of dead trees emergence should affect the competitive interactions between trees and thus affect selected productivity and stand structure indicators was not confirmed.

Therefore, we suggest that different patterns of dead tree emergence might not be considered in tree-based forest model, when basic growth, yield and stand structure indicators are to be evaluated. Still, effect on specific indices of horizontal stands structure (e.g. Clark & Evans 1954, Stoyan & Stoyan 1992), which might be more sensitive to the modified distribution of trees, need to be explored.

There are some limits of the interpretation of our findings related to the used experimental design. We assumed that the prescribed degree of spatial clustering of dead trees remains constant during the whole simulation period. This is, however, not a realistic assumption because various transitions between random and patchy tree mortality patterns are typical of bark beetle population dynamics. Typically, small populations generate a scattered pattern because the beetles search for suitable hosts, while beetles in large populations tend to infest the trees in a closer vicinity (Kausrud et al. 2011; Hlásny & Turčáni 2013). Large populations might tend to collapse after a several-year period of the outbreak culmination because of the effect of diverse density dependent regulation mechanisms (Raffa et al. 2008). Therefore, the coefficient of affinity we used in the current study should change in time depending on a number of factors (e.g. stand age structure) to mimic the real bark beetle dynamics more reliably. We, however, argue that such a complex processes can be better addressed by models that specifically explore bark beetle dynamics (e.g. Netherer & Nopp-Mayr 2005; Jönsson et al. 2012) or process-based forest models (e.g. Seidl et al. 2012), while empirical growth and yield-oriented models, such as that used in the current study, might prefer a simplified design such as that we described here.
Another limitation relates to the technical implementation of our module in the model Sibyla. Because the source code of the model is not publicly available, the disturbance mortality module (including tree species- and age class-specific mortality probabilities described in the text, and the dead tree clustering module) were developed as an independent application in the Python language. The application interrupts the forest development simulation, identifies the trees to die, and retrieves the output set-up to the model. Such an implementation is not that optimal, and it remarkably increases the computational time.

5. Conclusions

We presented here the testing of algorithm, which allowed to simulate various distributions of dead trees, which emerge during the development of spruce stands in the forest model Sibyla. Our study showed that the tested indicators of forest development were not sensitive to the altered distribution of dead trees in the stand and that the hypotheses on the effect of such an alteration on regeneration and increment were not confirmed.

Although the presented findings indicated that tree-based forest models might not consider specific patterns of dead trees emergence in forest stands, there are several limits related to the experimental design used in the current study, which require further investigation. These limits include, for example, the unknown sensitivity of the natural regeneration in the model to the modified stand density induced by the two tested mortality modes. Moreover, there are specific stand structure indicators, which can be more sensitive to tree distribution in a stand than the indicators evaluated here; the sensitivity of such indicators needs to be explored. Still, our study provided a new insight on the development of spruce forest stands in the forests model Sibyla and thus can support the optimized use of the model.

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Appendix A: Differences in the development of Norway spruce stand in the forest model Sibyla with the random and clustered occurrence of dead trees

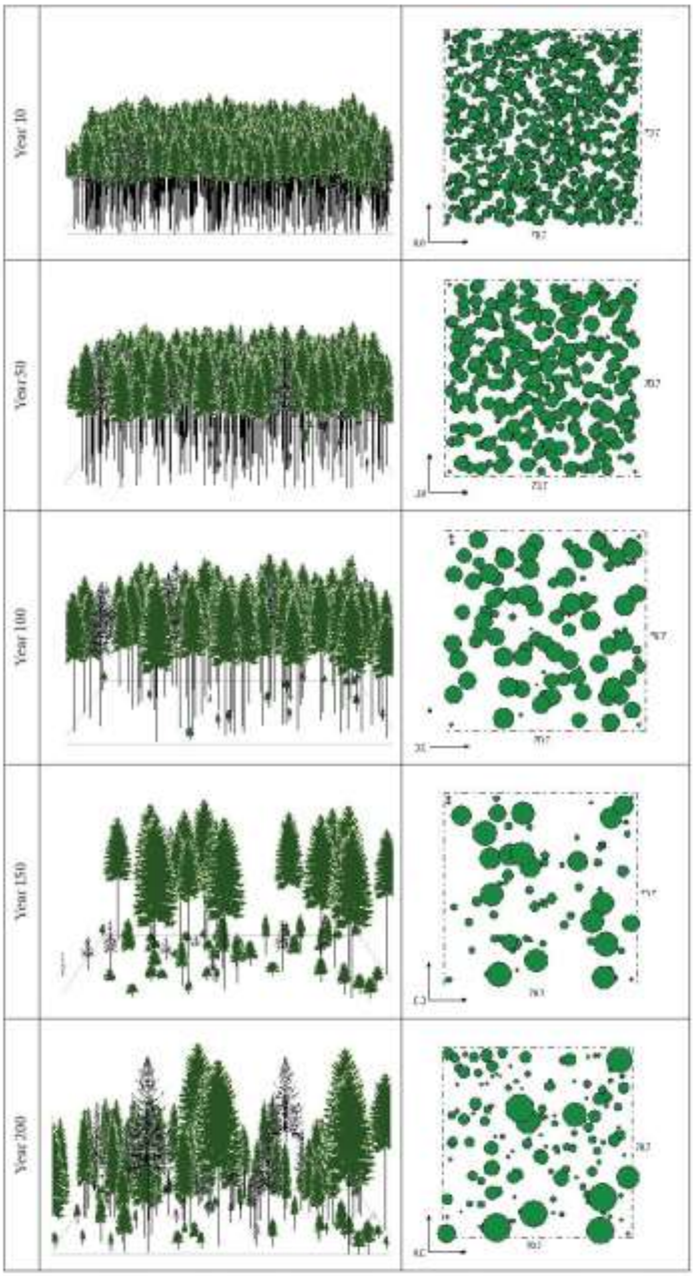

Fig. A1. Example of the development of spruce stand with the random occurrence of dead trees.

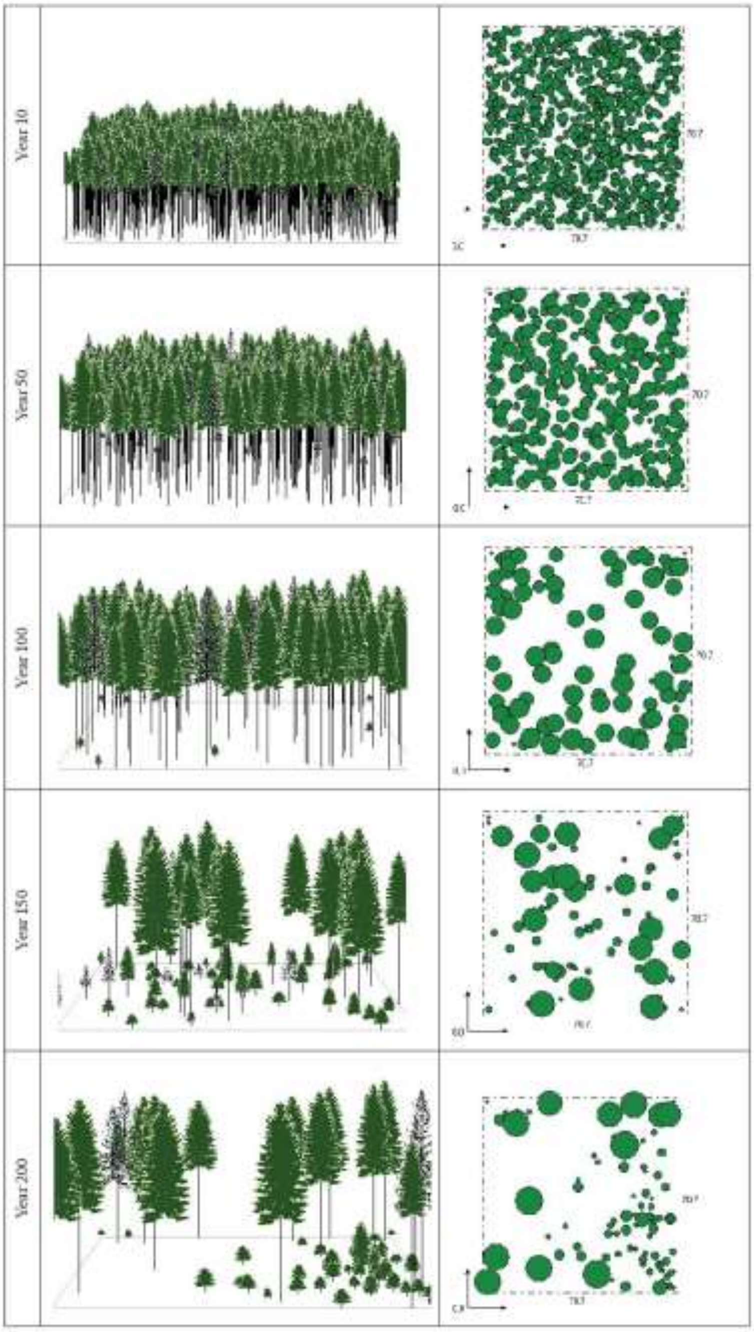

Fig. A2. Example of the development of spruce stand with the clustered occurrence of dead trees.

5.7 Conversion of Norway spruce forests in the face of climate change: a case study in Central Europe.

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ORIGINAL PAPER

Conversion of Norway spruce forests in the face of climate change: a case study in Central Europe

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Abstract Steadily increasing damage to Norway spruce forests in Europe has caused researchers and managers to consider whether these forests can be converted to more stable ecosystems. In a central European mountain region, we investigated whether management systems (MSs) specified by regional stakeholders provide sound alternatives to the currently applied management. We used the forest model Sibyla to explore whether the tested MSs differ in their sensitivity to climate change in terms of altered biomass production, stand structure, forest damage, and financial outcome. The tested MSs were no-management (NM), currently applied management (BAU), and management based on the preferences of forest managers (FM) or on the preferences of other stakeholders (OSH). With NM, spruce remained dominant during the simulation period 2010–2100, and the rate of damage significantly increased. Spruce also remained dominant with FM, while the abundance of non-spruce species significantly increased with BAU and OSH. The rate of salvage logging converged at 50% of the total harvest for all MSs up to 2050. Climate change reduced biomass production (−15%) with all MSs but had a negligible effect on biodiversity indicators. The average initial value of the simulated stands was 20,000 € ha^{-1} and the nominal value in 2100 was between 1900 and 10,900 € ha^{-1}. The Net Present Value calculated with the 2% interest rate was negative during the whole simulation period (−5600 to −18,500 € ha^{-1} in 2100). Effect of climate change on all financial indicators was negative. Our findings indicate that secondary spruce forests are highly vulnerable and that the systems proposed by both forest managers and other regional stakeholders failed to significantly reduce forest damage and stabilize forest production.

Keywords Biomass production · Forest diversity · Net present value · Forest modelling · Alternative forest management

Introduction

Man-made Norway spruce (*Picea abies* L. Karst) forests occupy a substantial part of the forest land in Central Europe (Spiecker et al. 2004). Although these forests are considered indispensable because they generate softwood timber, maintain biodiversity, moderate gravitation hazards, and support recreation, damage to these forests has been steadily increasing in recent decades (Hlásny and Sitková 2010; Briner et al. 2013), and their long-term sustainability has been repeatedly questioned (e.g. Grodzki 2010; Hlásny and Turčáni 2013; Hlásny et al. 2015a). Conversion of spruce stands growing on unsuitable sites to broadleaved or mixed stands has been one of the central

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issues of European silviculture in recent decades (Spiecker et al. 2004; Löf et al. 2010). The alternative management strategies usually include avoidance of clearcutting and of intense site-preparation techniques, fostering stand structure and tree species diversity, or promotion of natural regeneration (Puettmann et al. 2015). Such practices might reduce stand susceptibility to damage and increase tree survival (Griess et al. 2012; Jönsson et al. 2012; Neuner et al. 2014), which is particularly important in regions with intensifying disturbance regimes. Interest in these alternatives has increased also because of the growing recognition of forest multifunctionality (Gustafsson et al. 2012; Briner et al. 2013; Gamfeldt et al. 2013) and the increasing desire of diverse stakeholder groups to participate in forest management decisions (Phalen 2009; O'Brien et al. 2013; Shackelford et al. 2013; Sarvašová et al. 2014; Marzano et al. 2015). Stakeholder participation (e.g. via municipality or nature conservation representatives) in forestry decision-making, which has been uncommon in traditional forestry, might be particularly beneficial because it would provide regional expertise and would increase the public acceptance of the final outcome (Beckley et al. 2005).

Alternative management strategies that would address the ecological and environmental limits of forest exploitation as well as related financial risks have been increasingly scrutinized (e.g. Seidl et al. 2007, 2014; Lindner et al. 2010; Jactel et al. 2012; Ray et al. 2014; Schelhaas et al. 2015). The transition from traditional production-oriented forest management to alternative practices has received substantial attention in developed countries (Puettmann et al. 2015) but less attention in countries with transitional economies in Central and Eastern Europe. Particularly challenging is the transition from "even-aged, single-species-oriented management" towards "close-to-nature management"; the time required for such a transition is likely to exceed the time span of a rotation period (Roessiger et al. 2011). In the case of Norway spruce forests, which are the focus of this study, the current high market demand for softwood and the uncertain options for marketing the surrogate, mostly hardwood species are additional constraints to such forest conversion.

The modification of long-term management practices is particularly challenging in the face of climate change, which might both support and counteract the conversion efforts (Hlásny et al. 2014; Zlatanov et al. 2015). In Central Europe, the complex interactions between climatic stressors and the climate-sensitive dynamics of diverse pests represent the main climate change-related threat to regional forests (Thomas et al. 2002; Lakatos and Molnár 2009; Hlásny and Turčáni 2013; Klapwijk et al. 2013), and such interactions are likely to be amplified by climate change (Seidl and Rammer 2016). Climate change is expected to induce significant financial losses related to changes in species distribution, a deterioration of growing conditions, and an increase in damage (Kirilenko and Segjo 2007). For example, a shift towards less profitable species could reduce the economic value of current forest land by 28% by the year 2100 (Hanewinkel et al. 2012). Such effects can, however, differ along environmental gradients and management types. For example, Härtl et al. (2016) found that climate change slightly increased the economic return in an Austrian mountain region but slightly decreased the economic return in a Slovak mountain region.

In the current study, we used a modelling approach to analyse alternatives to traditional forest management in a central European mountain region. This region is part of a set of study areas in European mountains that are being investigated in a unified design in the 7th EU Framework Programme Project "Advanced Multifunctional Management in European Mountain Ranges" (ARANGE). The objectives of the current study were to determine whether management systems (MSs) specified by the regional stakeholders provide sound alternatives to the currently applied management. The reasons for searching for such alternatives are mainly related to (1) the increasing damage to the regional forests, the moderation of which apparently exceeds the capacity of current management; (2) the interest in increasing the financial profits generated by the forests; and (3) the interest in strengthening forest multifunctionality. The latter reason mainly concerns support of biodiversity, which has not been adequately supported by the current timber-oriented management even though biodiversity is positively associated with the quality of many ecosystem services and reduces susceptibility to damage (e.g. Díaz et al. 2006; Griess et al. 2012). We used a regionally adopted forest model to test whether the tested MSs differ in their sensitivity to climate change in terms of altered biomass production, forest damage rate, and stand structure. A particularly important objective was to evaluate the financial outcome generated by the MSs and how such financial outcomes will be affected by climate change. The research strives to extend our understanding of the development of secondary Norway spruce forests in Central Europe under climate change and to evaluate the risks and opportunities related to management strategies preferred by the regional stakeholders.

In support of these objectives, we tested the following hypotheses: (1) in spite of a high damage rate of spruce and in spite of climate change-mediated improvement of growing conditions for non-spruce species, spruce will remain dominant in the regional species composition; (2) climate change will reduce regional biomass production; (3) MSs that reduce the rotation period and increase species diversity will experience reduced damage because of the reduced stand susceptibility to most damaging hazards (Jactel et al. 2012; Griess et al. 2012; Morin et al. 2014);

and (4) the financial outcome generated by all MSs will decrease in the future because of ongoing damage and the adverse effects of climate change on forest productivity.

Data and methods

Study region and experimental design

The research was conducted in the Goat Backs mountain region of Slovakia, which has an area of 8226 ha and an elevation range of 650–1554 m a.s.l. The region has 62% forest cover dominated by Norway spruce (84%) (Fig. 1). Air temperature during the growing season (April–September) ranges from 12 to 15 °C, and growing season precipitation ranges from 380 to 510 mm. Cambisols and Podsols prevail, while Rendzinas occur on the calcareous bedrock at the highest elevations. Timber production constitutes ca. 95% of the regional forestry economy. Game hunting and recreation are other ecosystem services, which are actively utilized by the regional communities. More information about the region can be found in Hlásny et al. (2015a).

Forest development simulations for the period 2010 to 2100 were run for 25 forest stands, which were representative of stand and site conditions in the study area based on elevation, soil type, and tree species composition (Table 1; Fig. 1). The stands were selected based on forest management plans, forest soil maps, and a digital elevation model archived in the National Forest Centre, Slovakia.

In the forest dynamics model that was used (see the next section), the initial state of all stands was defined using diameter distribution functions and height curves for each tree species. Height and diameter data were collected in a field survey conducted in 2011 in each of the preselected forest stands. Specifically, three 0.045-ha plots per ha were

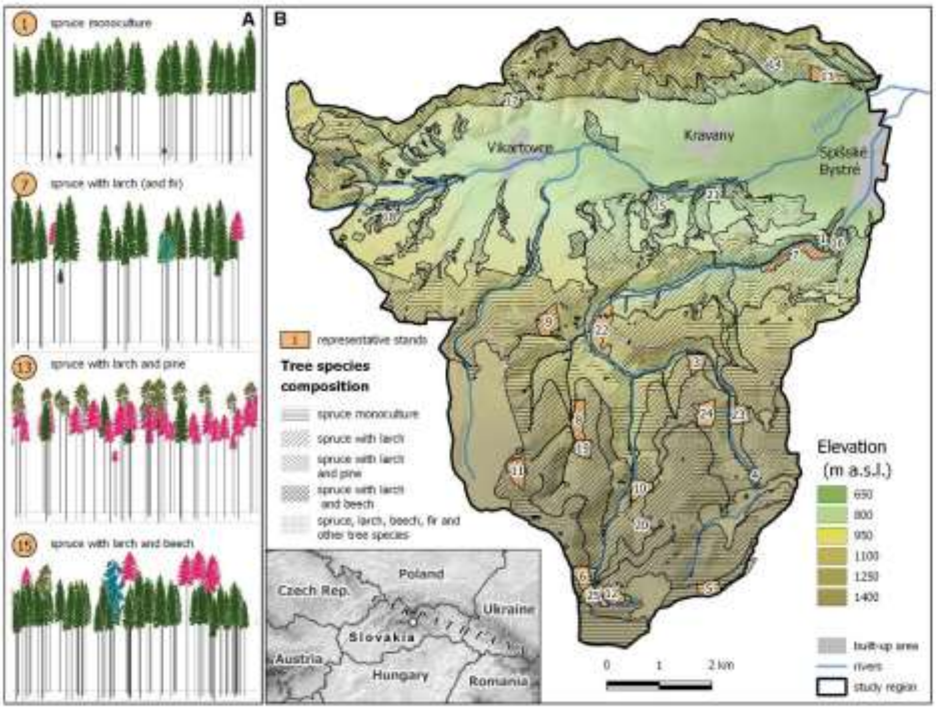


Fig. 1 Goat Backs Mts. model region. Tree species composition, elevation, and location of the 25 stands used for the simulation are indicated (stand codes are as in Table 1) (**a**). The initial state of four selected representative stands arranged on an elevational gradient is indicated as well (**b**)

Table 1 Criteria used to select the 25 representative stands for forest development simulations. Each combination of site and stand criteria is represented by a single stand

Species composition	Elevation (m a.s.l.)	Soil type	Stand ID
Spruce	600-800	Cambisol	1
	801–1100	Cambisol	2
		Podsol	3
	1101–1500	Cambisol	4
		Podsol	5
		Rendzina	6
Spruce with larch	600-800	Cambisol	7
	801–1100	Cambisol	8
		Podsol	9
	1101–1500	Cambisol	10
		Podsol	11
		Rendzina	12
Spruce with larch and pine	600-800	Cambisol	13
	801–1100	Cambisol	14
		Podsol	15
Spruce with larch, beech, and fir	600-800	Cambisol	16
	801–1100	Cambisol	17
		Podsol	18
	1101–1500	Cambisol	19
		Rendzina	20
Mixture of spruce, larch, pine, fir, beech, and maple	600-800	Cambisol	21
	801–1100	Cambisol	22
	1101–1500	Cambisol	23
		Podsol	24
		Rendzina	25

established in each stand to facilitate the calculation of the above parameters. Finally, the collected data were used to designate the virtual plots with size 200 × 12.5 m (0.25 ha). This rectangular shape was required to facilitate the simulation of harvesting operations, which are performed in parallel strips. Because information on tree positions was not available, the initial state of each plot was generated 15 times with different tree distributions while preserving the characteristic species mixture patterns observed in the stands. The results of the simulations were averaged and recalculated to per hectare units. To obtain regional estimates, the evaluated forest development indicators were weighted by the area of each of the 25 stand–site combinations occurring in the region (Table 1; Fig. 1).

The model

The simulations of forest development under four MSs and five climate scenarios were performed using the empirical forest dynamics model Sibyla (Fabrika and Ďurský 2005), the core components of which are based on the Silva model (Pretzsch et al. 2002). Sibyla is a tree-based model with a 1-year simulation step. The model has been repeatedly used in climate change impact studies in central European temperate forests by Hlásny et al. (2011, 2014, 2015a) and Härtl et al. (2016).

The model is suitable for studying the effects of climate change because several processes in the model are sensitive to climate. Tree growth is controlled by several ecological parameters, including six climate variables, which affect height and diameter increment through the modified site index (Table 2, Kahn 1994). Because species differ in their sensitivity to climate, climate change might modify competitive interactions between species and thus induce change in tree species composition [as was demonstrated by Hlásny et al. (2015a)].

Inherent tree mortality is indirectly sensitive to climate, i.e. changing the site index alters tree increment, which along with stand density and tree height (Ďurský 1997) determines the probability of tree death. If site conditions substantially worsen, inherent tree mortality might significantly affect the stand development. Contrary to inherent tree mortality, disturbance-related mortality was assumed to be insensitive to climate in the model. The mortality setting used was specific to tree species and age class, and was parameterized based on the forest disturbance records

Table 2 Projected changes in forest development drivers used in the forest dynamics model Sibyla

Driver	1980–2010	(2071–2100)–(1980–2010)	Mean and range of climate scenarios (2071–2100)
Atmospheric NO_x (ppb)	307.9	+18.9	326.8
Atmospheric CO_2 (ppm)	355.1	+69.7	424.8
Soil nutrients (0–1)[a]	0.35	–	–
Soil water content ($m^3\ m^{-3}$)[b]	0.29 (0.25–0.32)[c]	−0.08	0.21 ± 0.05
Number of days > 10° C (days)	138.0	+34.0	172.0 ± 56.0
Annual temperature amplitude (°C)	21.7	−0.8	20.9 ± 2.9
Mean temperature during veget. period IV–IX (°C)	12.2	+2.3	14.52 ± 3.8
Precipitation totals during veget. period IV–IX (mm)	518.0	−70.0	447.0 ± 364.0
de Martone aridity index (mm °C^{-1})[d]	23.3	−4.9	18.4 ± 13.4

Mean and range of five climate change scenarios are given for each climate variable. The data are for 950 m a.s.l. elevation, but the variability of projected changes along the elevation gradient is low

[a] Soil nutrients were derived from soil characteristics and were not subject to any changes during the simulation period

[b] Soil moisture development was simulated individually for each stand using daily climate data and soil properties using the hydrological model ISSOP (Hlásny et al. 2015b)

[c] Range of the soil water content for the simulated stands

[d] (Precipitation totals during vegetation season)/(mean temperature during vegetation season + 10)

for the period 1998–2009 using the data from the whole of Slovakia (Hlásny et al. 2015a). The used disturbance mortality rates consider an aggregate effect of all disturbances in the region. The model uses the mortality rates derived from the national statistics to determine the mortality rate for each single tree in a stand based on species and age, and evaluates stochastically whether or not a tree dies. This approach can induce bias in mortality estimates, because damage rates derived from records on stand damage (whole or partial) are applied at the scale of a tree. This bias, however, should be reduced by averaging the simulation outputs over a number of stands and simulations, as was done here.

Regeneration is another process indirectly sensitive to climate. Regeneration density is driven by several constant tree species-specific parameters (seed production, germination rate, etc.) and by other parameters that change during stand development (stand density and site conditions, which also include climate). Climate effects on species-specific regeneration density were calculated based on the Slovak National Forest Inventory data (Merganič and Fabrika 2011). Climate change might also affect regeneration based on climate-mediated changes in the growth and inherent mortality of the mother stand. Both natural and artificial (i.e. planting) regeneration modules were activated during the simulation; MS-specific artificial regeneration rates are indicated in Supplementary Material C.

Management is implemented in the model in terms of stand age, diameter classes, and proportions of stocking volume to be extracted in individual years of the simulation period. A number of thinning and harvesting techniques, which are commonly applied in Central Europe, can be activated.

Forest development drivers

Outputs of five regional climate models (which were driven by the emission scenario A1B) and a statistically generated stable climate (corresponding to the period 1980–2010 and referred to as the baseline climate) were used to drive the forest development simulations. For details of the downscaling approach, see Bugmann et al. (2017) and Supplementary Material A. The scenarios are referred to as c1–c5 and are ordered according to the magnitude of the projected air temperature increase. The IPCC SRES A1B scenario (Nakicenovic and Swart 2000) was used to describe the future development of CO_2 emissions. The evolution of nitrogen deposition was based on Dentener (2006). The changes in forest development drivers used in the model between the period 2071–2100 and 1980–2010 are indicated in Table 2.

Evaluated management systems

Four MSs were investigated. Two of the MSs (FM and OSH) represent alternatives to the currently applied MS (BAU) and were designed based on communication with the Regional Stakeholder Panel (RSP), which was established in the 7FP EU Project ARANGE. The RSP consisted of eight persons representing public authorities, non-governmental organizations, and community members, and six

Table 3 Basic characteristics of the investigated forest management systems

Management system	Management type	Target age structure	Rotation period (years)	Final cut	Final cut area (ha)	Planting	Target tree species
NM	–	Uneven	–	–	–	–	–
FM	Rotation	Even	90	Shelterwood	<3.0	No	Spruce
BAU	Rotation	Even	100	Shelterwood	<3.0	Non-spruce species	Spruce, larch, fir, beech
OSH	Continuous cover	Uneven	>120	Shelterwood to selection	<0.02	Non-spruce species	Spruce, fir, beech

BAU currently applied management, *FM* management system based on the preferences of forest managers, *OSH* management system based on the preferences of other stakeholders, *NM* no-management system

persons representing forest owners and managers (see Supplementary Material B for details). The MSs were designed based on a questionnaire that identified stakeholder opinions on the forces driving management decisions in the region and on the prospects of the regional forests (Supplementary Material C). Researchers then transformed the questionnaire responses into MS descriptions, which were then implemented in the forest dynamics model.

BAU is an even-aged, uniform, shelterwood system that emphasizes timber production and an ongoing reduction in the share of spruce. The FM system is based on the preferences of regional forest managers and has a strong focus on financial indicators and on the maintenance of a high share of spruce. The OSH system is based on the preferences of other stakeholders, such as the municipality representatives and nature conservation organizations, and promotes close-to-nature management with emphasis on forest diversity, extended rotation and regeneration periods, and small-scale interventions that do not substantially open the canopy. In addition, unmanaged forest development (NM) was evaluated (Table 3). Detailed information about the four MSs and the stakeholders participating in MS definition is provided in Supplementary Material B and C.

Evaluated indicators

The ability of the tested MSs to modify the current tree species composition was evaluated based on the changes in species-specific aboveground biomass volume in standing trees (V). The total production of aboveground biomass (TVP) was evaluated as cumulative volume of aboveground biomass (stem, branches, trunk, foliage) regardless of whether it was harvested or not. The volume of tree compartments was calculated based on the equations proposed by Petráš et al. (1985) and Petráš and Pajtík (1991). The cumulative volume of dead wood generated by both disturbance and inherent tree mortality (i.e. the dead wood component of the TVP, which is referred to as TVP-D) was evaluated as an indicator of MS capacity to moderate forest damage. The ratio of salvage and total (salvage plus planned) harvested volume was used as an additional variable indicative of the effect of MS on damage rate.

Tree species diversity was evaluated using the true diversity index D (Jost 2006), which is the exponential form of Shannon's diversity index S:

$$\begin{cases} S = -\sum_{i=1}^{N} p_i \ln(p_i) \\ p_i = \frac{d_i}{G} \end{cases}$$

where N is the number of species, d_i is the basal area of species i (m^2; in this study calculated using the basal area of tree species with diameter ≥5 cm), and

$$G = \sum_{j=1}^{S} g_j (\mathrm{m}^2)$$

Hence, the true diversity index D is defined as:

$$D = \exp(S)$$

Tree size diversity index H was evaluated based on the post hoc index presented by Staudhammer and LeMay (2001):

$$\begin{cases} H_{\mathrm{size}} = \frac{H_{\mathrm{DBH}} + H_{\mathrm{H}}}{2} \\ H_{\mathrm{DBH}} = -\sum_{i=1}^{N_{\mathrm{DBH}}} \frac{g_i}{G} \ln\left(\frac{g_i}{G}\right), \\ H_{\mathrm{H}} = -\sum_{i=1}^{N_{\mathrm{H}}} \frac{g_i}{G} \ln\left(\frac{g_i}{G}\right) \end{cases}$$

where N_{DBH} and N_{H} are the number of DBH and height classes present in the stand, g_i is the basal area (m^2) of DBH or height class i, and G is the basal area of the stand (m^2). We used 5-cm classes for DBH and 2-m classes for height (Cordonnier et al. 2013).

The dead wood volume, which is commonly used as an indicator of biodiversity (e.g. Lassauce et al. 2011), was not evaluated because all managed systems strive to remove the dead wood instantly in order to avoid supporting bark beetle populations.

The financial viability of the MSs was evaluated using the net present value (NPV) generated during the simulation period, which is defined as the sum of all discounted net revenue flows. We used a modified NPV definition by Klemperer (1996), which allowed us to compare NPV generated by the MSs during the simulation period, which differs from the rotation cycle (Table 3) (e.g. Roessiger et al. 2016). Instead of calculating only a single NPV for the entire simulation period (2010–2100), we calculated NPV as a sequence of periods starting from year 0 of the simulation period (2010) and incrementally increasing in 5-year steps to 2100 (i.e. the periods 2010–2010, 2010–2015, 2010–2020…, 2010–2100). Each NPV calculation included the discounted net revenue flows incurred during the respective period and the discounted difference between the financial stand value at the end of each period (i.e. years 2010, 2015, 2020, etc.) and the initial stand value in year 2010.

For the sake of simplicity, we also use the term NPV for the financial outcome generated by NM, where only the difference between the discounted financial stand value at the end of the simulation period and the initial stand value was considered (i.e. without any revenue flows). The applied interest rate was 2%.

To facilitate this analysis, we collected timber prices and harvesting costs, silviculture costs, and afforestation costs for all management operations for each MS (Supplementary Material D). To calculate the NPV, we summed the discounted net cash flows of each silvicultural and harvest operation conducted during the simulation period (2010–2100) and weighted them by stand area.

Results

Change in tree species composition

Simulations driven by the baseline climate data (i.e. not affected by climate change) showed that the proportion of non-spruce species, in terms of species-specific biomass volume, slightly increased with NM (Fig. 2a). While most species preserved their initial percentage of representation during the simulation, silver fir (*Abies alba* Mill.) increased substantially (from ca. 2 to 8%). At the end of the simulation period, the spruce proportion decreased from the initial 87 to 78%.

The FM system also preserved a high percentage of spruce; the difference between the initial and final percentage was only −5%. The share of fir increased in the FM system, and the increase was greater (from 2 to 13%) than in the NM system.

Even though the underlying management principles were different, the BAU and OSH systems showed surprisingly similar development of species percentages. The percentage of spruce decreased from an initial value of ca. 87 to 47% with BAU and to 41% with OSH. The percentages of beech (*Fagus sylvatica* L.), silver fir, and maple (*Acer pseudoplatanus* L.) increased with both BAU and OSH.

Climate change accelerated the decrease in the percentage of spruce with all MSs and generally accelerated the change in tree species composition (Fig. 2b). Climate change caused an additional decrease in the percentage of spruce by up to 3% with NM and by up to ca 10% with BAU, FM, and OSH.

Total volume production

The TVP simulated under the baseline climate differed only slightly among the MSs by the end of simulation period (Fig. 3). The TVP was smallest with FM (638 $m^3\ ha^{-1}$) and was highest with NM (685 $m^3\ ha^{-1}$). The per-species TVP corresponded to the changes in species composition described earlier: by the end of simulation period, the non-spruce species accounted for 10% of the TVP with FM but for 15–24% of the TVP with the other MSs.

The response of TVP to climate change differed greatly among climate change scenarios with all MSs. While the moderate scenarios, c1–c3, induced TVP changes ranging from +2 to −7% relative to the baseline climate simulations, the two severe scenarios, c4 and c5, caused decreases in the TVP from −12 to −18%. The decrease was greatest with FM.

Tree species and size diversity

The evaluated diversity indices responded differently to the four MSs (Fig. 4). With NM, tree species diversity *D* remained unchanged, but tree size diversity *H* increased steadily throughout the simulation period. FM caused only a minor increase in *D*, while OSH and BAU caused a substantial increase in *D*. OSH and FM caused a minor increase in H, while BAU caused a substantial increase in *H*. Thus, the most positive effect on both indices was obtained with BAU management.

Climate change affected *D* and *H* only marginally. While the divergence in simulations driven by the five climate change scenarios was low with NM, both positive and negative responses were simulated with the other MSs. The most distinct response was the climate change-induced increase in *D* with FM.

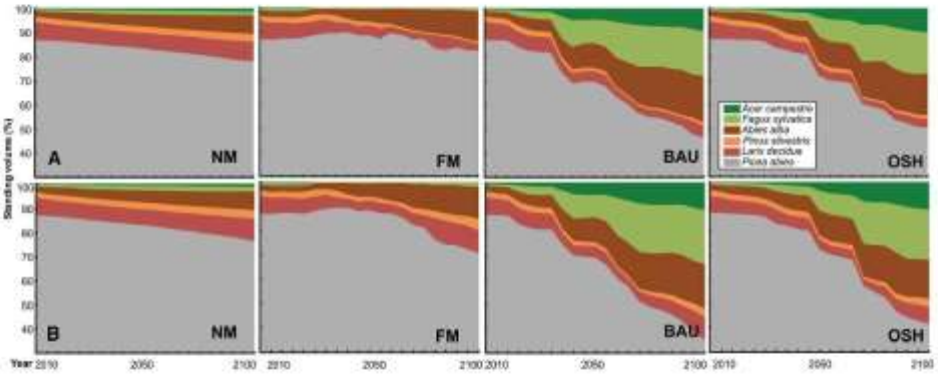


Fig. 2 Development of tree species composition in terms of the relative standing volume of main forest tree species (% of the total standing volume) under four management systems. Row A shows simulations driven by the stable climate referring to the period 1981–2010, and row B shows average of simulations driven by five climate change scenarios. Management codes: *NM* no-management, *FM* management based on the preferences of forest managers, *BAU* currently applied management, *OSH* management based on preferences of other regional stakeholders

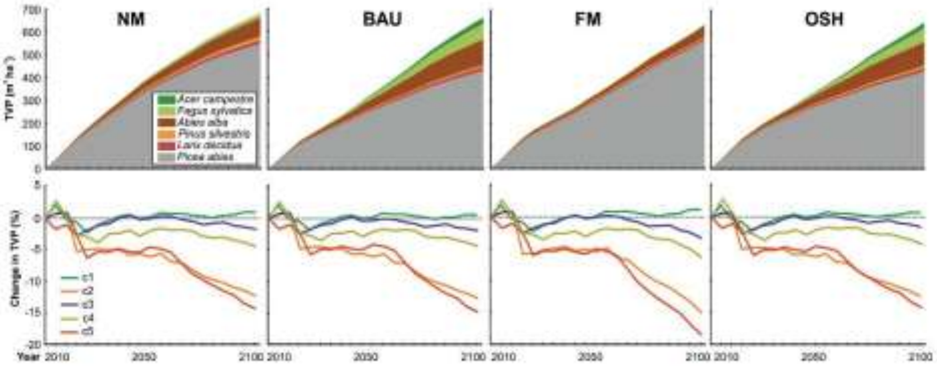


Fig. 3 Total volume production (TVP) per tree species simulated under a baseline climate (*upper row*), and change in TVP averaged for all tree species simulated under five climate change scenarios (c1–c5) (*lower row*) for four management systems (management codes are described in Fig. 2)

Forest damage

Because we assumed that the parameters of species- and age class-specific disturbance rates were stable during the simulation period, and because the relative effect of inherent mortality on the total amount of damaged wood was marginal under all climate change scenarios, only simulations driven by the baseline climate are presented (Fig. 5).

TVP-D was almost two times higher with NM than with the managed systems (871 vs. 454–500 m^3 ha^{-1} during the simulation period); differences among the managed systems were negligible (±5%). In addition, TVP-D accounted for 72% of the TVP with NM but only for 38–43% of TVP with managed systems (Fig. 5a). TVP-D began to diverge between the NM and the managed systems after ca. 2020.

Despite differences in the underlying principles of the MSs, the ratio of salvage and total harvested volume generated by the managed systems converged at 50% in 2070 and remained stable during the rest of the simulation period (Fig. 5b). The differences between MSs were

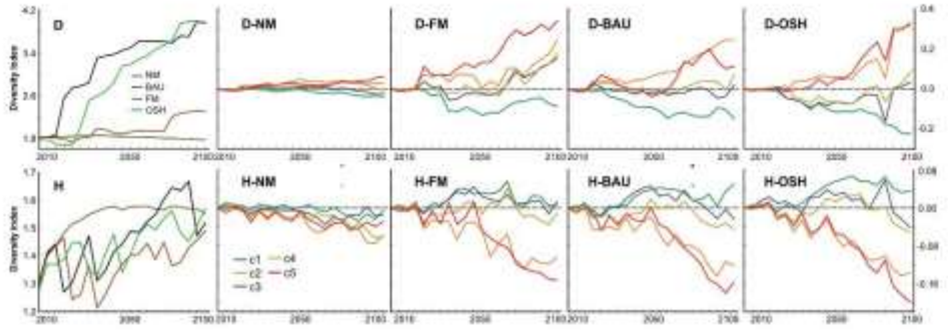
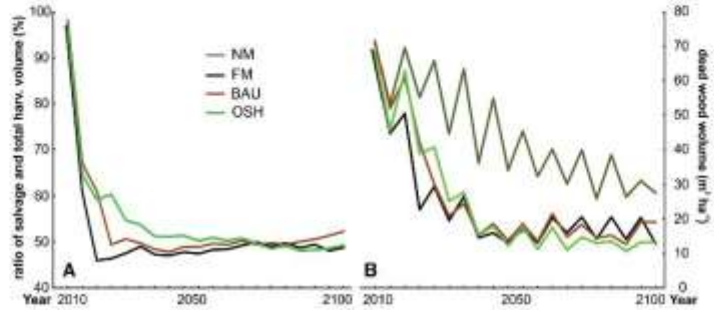


Fig. 4 Tree species diversity index D and tree size diversity index H simulated during the period 2010–2100 with four management systems. Panes D and H indicate the development of the indices under the baseline climate. The remaining panes show the difference between simulations driven by climate change scenarios (c1–c5) and the baseline climate. Management codes are described in Fig. 2

Fig. 5 Ratio of salvaged and total harvested volume simulated under three management systems (**a**), and dead wood volume simulated under four management systems (**b**). The simulations were driven by the baseline climate corresponding to the period 1981–2010. Management codes are described in Fig. 2



greatest mainly during the period 2015–2060; with BAU, for example, the ratio had already reached ca. 45% by 2020.

Net present value

The mean initial value of all simulated stands was 20,000 € ha^{-1}. The simulations show that NPV was negative during the entire simulation period with all MSs (Fig. 6), which indicates that the discounted costs of management operations exceeded the revenues; the NPV ranged from −5600 to −18500 € ha^{-1} in year 2100, depending on MS. The largest drop in value was with NM, where dead wood decomposed without generating revenue. Hence, the value −18,500 € ha^{-1} reflects a high rate of damage typical of NM (Fig. 5) and indicates that the stands were rather disintegrated in 2100.

To better compare NM with the managed systems, we proposed a modified NM ($NM_{salvage}$) that considered the dead wood generated during the simulation as the revenue; NPVs for both NM and $NM_{salvage}$ are displayed in Fig. 6. The analysis showed that the NPV in 2100 was −8400 € ha^{-1} with $NM_{salvage}$, but the NPV had converged to −5860 € ha^{-1} ± 2% with all of the managed systems.

A detailed analysis of processes behind the negative NPV showed that most harvests occurred at the beginning of the simulation period, because 43% of the forest stands were initially 100–110 years old. Specifically, the average planned harvest rate was 4.9 m^3 ha^{-1} $year^{-1}$ up to 2050, and then decreased to 1.5 m^3 ha^{-1} $year^{-1}$. Obviously, the harvest of mature trees contained a high share of salvage logging. For the managed systems the mean annual volume of salvage logging was 5.6 m^3 ha^{-1} to 2050 and then

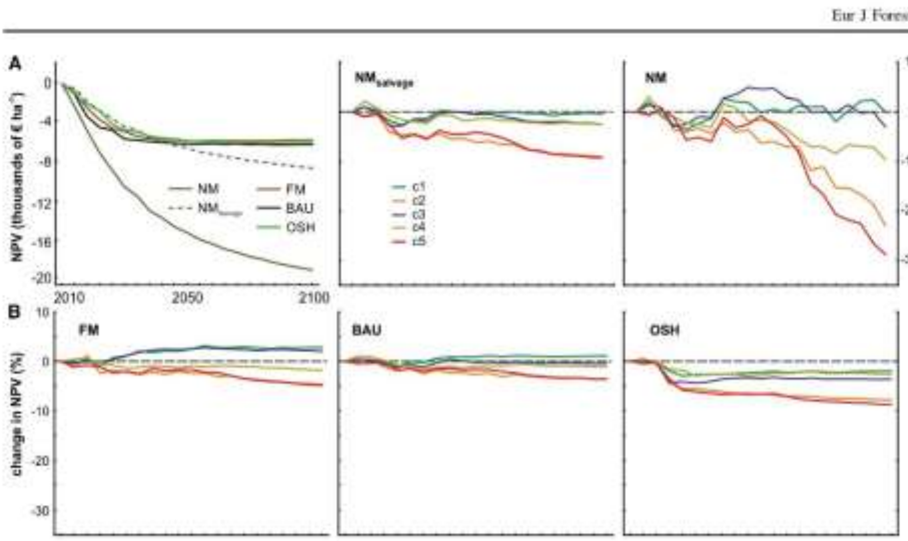


Fig. 6 Net present value (NPV) calculated for a sequence of time periods over the simulation period (from 2010–2010 to 2010–2100) generated by four management systems (**a**) and the relative response of NPV to five climate change scenarios. For an improved comparison of NPV generated with managed and unmanaged systems, a hypothetical example is also presented for the NM in which the dead wood generates revenues ($NM_{salvage}$)

1.6 m^3 ha^{-1} in the remaining period, i.e. it exceeded the planned harvests.

A theoretical exercise showed that if the salvage logging is assumed to have the parameters of regular harvests, the NPV in 2100 would have been −400 € ha^{-1} with BAU; 2200 € ha^{-1} with FM; 700 € ha^{-1} with OSH; −18,500 € ha^{-1} with NM; and 8800 € ha^{-1} with $NM_{salvage}$.

With the three managed systems and $NM_{salvage}$, NPV was reduced by climate change by up to 5% (average of five climate change scenarios) (Fig. 6). The decrease was greatest with OSH and $NM_{salvage}$ (−5%) and was ca—1.5% with FM and BAU. While the decrease in NPV was only slightly greater with $NM_{salvage}$ than with the managed alternatives, the decrease with NM was larger (on average 13%). This, however, can be considered an artefact because the NPV calculation for NM uses only the final stand value in year 2100, which is greatly influenced by climate change. In contrast, NPV for the remaining MSs consists of a number of single cash flows that occurred during the whole simulation period.

As the complementary information, we calculated the nominal value of the remaining stand in 2100, which had an initial average value of 20,000 € ha^{-1} in 2010. In 2100, the average of baseline climate simulations produced the value of 10,864 € ha^{-1} for NM, while it was only 2962 € ha^{-1} for FM, 2019 € ha^{-1} for BAU and 1908 € ha^{-1} for OSH. Extremely low values for the managed systems were mainly related to the decline of overmature stands during the first half of the simulation period, continuous removal of dead trees, which resulted in a low standing volume and an increased share of less productive species. Effect of climate change on the value of the remaining stand was more pronounced than the effect on NPV. The reduction was 13% for NM, 32% for FM, 22% for BAU and 20% for OSH.

Discussion

In this study, we investigated the development of a central European mountain forest as affected by several management alternatives and climate change. The research was motivated by the growing concern about the future of commercial forests dominated by Norway spruce and by the growing desire to convert such forests to ones that are better adapted to environmental change (Spiecker et al. 2004; Löf et al. 2010; Hlásny et al. 2015a). Although management obviously plays a key role in mitigating the effects of climate change on such forests (Bravo et al. 2008), the possible development trajectories remain largely unexplored (Bugmann 2014). We investigated forest development indicators of ecological and commercial importance and the responses of such indicators to management and climate change. In this section, we discuss the ability of the investigated MSs to help forests adapt to climate change, and we also discuss the limitations of our approach.

Unmanaged forest development

Most forest stands investigated in the current study were secondary, i.e. they were established by foresters and in many cases were not well suited to site conditions. The poor prospects for this kind of forest raises the question as to whether unmanaged development might enable natural processes to restore the original species composition of the forests as was suggested, for example, by Drever et al. (2006). Our simulations indicated that this was not the case for the study region, at least not in the time span of the simulation period. With NM, spruce remained dominant, and damage remained high. Our simulations showed that the frequent disturbances, which open the canopy, supported the regeneration of spruce and that deciduous species appeared only slowly, which was consistent with observations of Drobyshev (2001). The slow rate of change agrees with Schelhaas et al. (2015), who suggested that European forests are very inert and that altering their species composition requires a long time. In the study area, this inertia is apparently related to the regeneration success of spruce, even though climate change increasingly favours the non-spruce species (Hanewinkel et al. 2012; Hlásny et al. 2011, 2015a; Schelhaas et al. 2015). The simulated regeneration success of spruce agrees with observations in the study region and in other regions (e.g. Ulbrichová et al. 2006).

Tree species diversity remained low during the whole simulation period, while the diversity of tree size significantly increased, providing potential benefits to biodiversity through the increased diversity of habitat (Staudhammer and LeMay 2001). Diversity indices were only marginally affected by climate change. Interestingly, the inter-climate model variability of *D* and *H* was significantly lower with NM than with the managed systems, which implies that the predictability of stand structure indicators is better with unmanaged development than with managed development

The increase in the abundance of dead wood in NM, which is periodically removed in the managed systems, can support biodiversity (Lassauce et al. 2011). In spruce forests, however, increased abundance of dying and newly dead trees supports bark beetle populations (Økland and Berryman 2004; Hlásny and Turčáni 2013), which have been severely damaging the regional forests in recent decades (Hlásny and Sitková 2010; Kunca et al. 2015). Therefore, the coupled effect of dead wood accumulation and climate change-induced acceleration of bark beetle development (Jönsson et al. 2007; Berec et al. 2013) might be devastating for the regional forests. In fact, substantial forest deterioration, which was manifested by the simulated drop in the value of the remaining stand in 2100, occurred even though the applied disturbance mortality rates were derived from the period 1998–2009 and therefore without the amplifying effect of future climate change (e.g. Seidl and Rammer 2016).

For the above reasons, we argue that one cannot expect that application of a no-management regime will stabilize secondary forests or significantly increase conservation values within the period of ca. 100 years; instead, the unmanaged development is likely to accelerate the ongoing forest decline.

Managed forest development

The currently used management system, BAU, does to some degree support forest conversion by including the planting and protecting of non-spruce species. BAU performed very well in our simulations with regard to tree species composition (i.e. spruce proportion decreased from 87 to 47%) and stand diversity as indicated by *D* and *H* indices. Still, the rate of salvage felling remained greater than 50% of the total harvests, which represents a significant obstacle to forest management and highlights the need for more radical interventions.

FM reflected the desire of forest managers to produce softwood timber and to reduce planting costs. FM also reflected the expectation of forest managers that a reduction in the rotation period might help sustain spruce-oriented management (Schelhaas et al. 2010; Lagergren and Jönsson 2010; Sedjo 2010). It is interesting that in spite of the good performance of BAU in our simulations, forest managers tended to favour an increased emphasis on spruce and a reduced effort to introduce non-spruce species, i.e. the forest managers tended to favour practices that promised to maintain short-term profitability. However, our analyses of the financial outcome failed to indicate that NPV would be greater with FM than with the other MSs. The reduction from a 100-year rotation period for BAU to a 90-year rotation period for FM is unlikely to substantially increase forest stabilization, particularly given the age-dependent disturbance-related mortality rates used in our study (Hlásny et al. 2015a). These rates indicate that there is about 70% probability for a spruce stand to be destroyed up to the age of 90 years. Given that bark beetles have been responsible for ca. 40% of the total forest damage during the recent decade (Kunca et al. 2015) and that bark beetles typically attack trees older than 70 years (Wermelinger 2004), a 70-year rotation period could be considered. Such a rotation is applied, for example, in Croatia (Matić et al. 2010) and in some Baltic and Nordic countries (Rytter et al. 2013). This reduction in the length of the rotation period, although well justified, might not be acceptable because of a strong persistence of traditional practices as well as a temporary surplus of harvested timber that could exceed the wood-processing capacities (Lindner et al. 2008).

OSH was mainly driven by the interest in recovering natural processes. OSH attempts to support biodiversity (by planting admixed tree species), forest aesthetic value and promotes long rotation periods and small-scale interventions. This approach was effective in changing the forest species composition because spruce percentage decreased to only 41% in the last year of the simulation. On the other hand, the longer rotation periods, which increased the abundance of vulnerable overmature trees, caused a high rate of salvage logging to persist longer than with BAU and FM (Schelhaas et al. 2010). Such development might imply a positive effect of disturbances on changes in species composition and biodiversity (Müller et al. 2008; Thom and Seidl 2015), i.e. the disturbances might provide opportunities for more climatically adapted species to establish (Buma and Wessman 2013). In the long run, the small-scale interventions of OSH might better support asynchronous forest dynamics than the other systems and thus support the forest's inherent adaptive mechanisms (Morin et al. 2014).

In all MSs, climate change- and disturbance-mediated support to biodiversity should be considered as an opportunity in forest adaptation efforts in spruce dominated stands. Indeed, adverse effects such as the presented decrease in productivity by up to 15% or support to bark beetle outbreaks (Jönsson et al. 2007; Fleischer et al. 2016) must not be marginalized.

Forest financial value

The complexity of our approach was increased by considering the effect of management and climate change on the financial outcome. Studies on the anticipated effect climate change on forest NPV are scarce (e.g. Hanewinkel et al. 2012; Borys et al. 2015), and this limits our ability to compare our findings with those of other studies. However, information on financial losses and gains can be particularly supportive of management decisions under climate change (Bravo et al. 2008; Eliasch 2008) and can be effective in convincing forest managers to invest in forest adaptation.

Minor differences in NPV development between the tested MSs showed that NPV was not very sensitive to the intensity and timing of the management operations. It is noteworthy that while future forest production was predicted to be greatly affected by climate change, this did not directly translate to changes in NPV because of a strong discounting effect in the distant future; for c4 and c5 climate change scenarios, the TVP decreased by up to 18% while NPV decreased by 0–8% for all MSs. This implies that NPV was mainly affected by a high rate of salvage operations rather than by differences in MSs or by climate change-induced decrease in forest productivity.

A substantial part of NPV in all MSs was derived from the income generated from damaged spruce wood. We found that the NPV could have been ca. 30–40% higher if timber prices had not decreased because of the damage and if the harvesting costs had not increased due to salvage operations. This suggests that reducing the damage by both decreasing inherent forest vulnerability and increasing the efficiency of forest protection is important in the region and might even compensate for losses in biomass production induced by climate change. As Thom et al. (2013) suggested, however, the response of the forest disturbance regime to management can be rather delayed, which underscores the difficulties in stabilizing the regional forests.

The adopted discount rate of 2% should be considered as an assumption; such a value was used, for example, by Roessiger et al. (2011, 2013), while both lower and higher values were used by other authors (e.g. Brunette et al. 2014). The discount rate significantly affected the estimates of NPV in the current study; for example, a discount rate of 0% caused NPV to increase monotonously during the simulation period for all MSs except for NM (data not shown), which is opposite to the presented results. Therefore, the presented decrease in NPV should be considered as strictly specific to the applied discount rate.

Methodological advances and limitations

The complexity of the employed modelling approach generates concerns about the reliability of the estimates for use in forestry decision-making (Yousefpour et al. 2012; Lindner et al. 2014). Among the whole "cascade of uncertainty" (Lindner et al. 2014), the only uncertainties we considered involved climate change scenarios and stochasticity in stand initialization (i.e. 15 replicates); stand initialization, however, only marginally affects the uncertainty of final estimates (Hlásny et al. 2014). It is possible that we significantly underestimated uncertainty of final estimates by adopting only one assumption regarding disturbance-related mortality and by using only one forest model; these factors were found to substantially affect the variability of modelling output (Hlásny et al. 2014; Horemans et al. 2016). Such an underestimation of uncertainty might induce overconfidence in the presented results and potentially lead to poor decisions, such as an inadequate consideration of reversible and flexible management options (Hallegatte 2009; Seppälä et al. 2009). On the other hand, the credibility of our results is supported by our use of highly realistic definitions of applied silviculture and harvesting operations and by previous findings that management greatly affected the variability of modelling outputs (e.g. Hlásny et al. 2014; Horemans et al. 2016).

The model that we used has been repeatedly tested against observed data (e.g. Schmid et al. 2005; Hlásny et al. 2011, 2014; Bošeľa et al. 2013; Horemans et al. 2016), and tree growth performed well in most of the distribution of investigated tree species. However, the model has not been tested at extreme sites, and its performance under poor growing conditions (e.g. those induced by the c5 scenario at water-limited sites) is unknown. This is, however, a limitation of most models (Anderegg et al. 2015) and must be considered in the interpretation.

We assumed that parameters of species- and age class-specific disturbance-related mortality were stable during the entire simulation period (i.e. specific to the period 1998–2009) despite the proven increase in climate-induced tree mortality (van Mantgem and Stephenson 2007), which is expected to be further amplified by climate change (Seidl et al. 2015; Seidl and Rammer 2016). This assumption was adopted because the empirical approach to forest modelling that we used is unable to simulate the complexity of future disturbance regimes and thus cannot provide reliable estimates of the future damage to forests. The damage rates that were used characterize the disturbance regime during damage culmination phase of 1998–2009 (Hlásny et al. 2015a), and were thus considered to represent a reasonable and plausible estimate of future development. Still, the underestimation of variability in simulation output related to this assumption, and the respective consequences for forestry decisions, needs to be considered as discussed above.

The presented changes in forest development indicators induced by climate change represent a mixture of positive and negative responses, which usually occur along an elevation–climatic gradient and which have been reported from diverse environments (e.g. growth and productivity decline in the dry–warm part of the gradient and increase in the cool–moist part of the gradient) (Hlásny et al. 2011, 2015a; Mina et al. 2015; Zlatanov et al. 2015; Pardos et al. 2016). We, however, presented an aggregate response that can be relevant for regional management planning, particularly for assessing future biomass production and financial outcome on a scale of a larger management unit.

Because the applied management operations were differentiated based on stand and site conditions (including elevation), and because simulation outputs were weighted by the total area associated with each of the 25 simulation stands (i.e. area of each combination of stand and site, Fig. 1; Table 1), the presented aggregate information provides a reliable regional estimate of the evaluated indicators and their response to climate change. However, that we represented the forest development of the entire study area by simulating 25 stands unrealistically synchronized forest development. This, however, should not detract from our inferences, which mostly relied on comparison between managements and/or climate change scenarios.

Conclusions

Our study evaluated the combined effect of climate change and four forest management systems on various aspects of forest development in a mountainous region in Central Europe. Although two management systems were proposed by the regional stakeholders as alternatives to the currently applied management, our simulations indicate that forest management based on the stakeholder views will fail to substantially improve future forest production, damage, or financial value relative to the current management. At the same time, it is obvious that a reduction in the current high damage rate and adaptation to climate change will require substantial modifications of the current system. Our findings indicate that the transition from the current even-aged spruce-oriented management to management that promotes more diverse stands, shorter rotations, and smaller-scale interventions might be a viable alternative that would support sustainable, multipurpose forests, and their adaptation to climate change.

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CONVERSION OF NORWAY SPRUCE FORESTS IN THE FACE OF CLIMATE CHANGE: A CASE STUDY IN CENTRAL EUROPE

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SUPPLEMENTARY MATERIAL A: USED CLIMATIC DRIVERS

We used five climate change scenarios, which were selected from the 22 scenarios developed in the ENSEMBLES project (van der Linden and Mitchell 2009) to cover the uncertainty range of the original data set. Observed climate data collected from 19 meteorological stations during the period 1961–2009 were used for scenarios downscaling and for the creation of a stable (baseline) climate. Here, we present the development of climate variables that drive forest development in the model Sibyla according to the five climate change scenarios. The couples of General Circulation Models and Regional Climate Models specific to the five climate change scenarios are: c1: DMI-HIRHAM5 – BCM, c2: DMI-HIRHAM5 – ARPEGE, c3: ICTP-RegCM – ECHAM5-r3, c4: SMHI-RCA – ECHAM5-r3, and c5: HC-HadRM3 – HadCM3Q16.

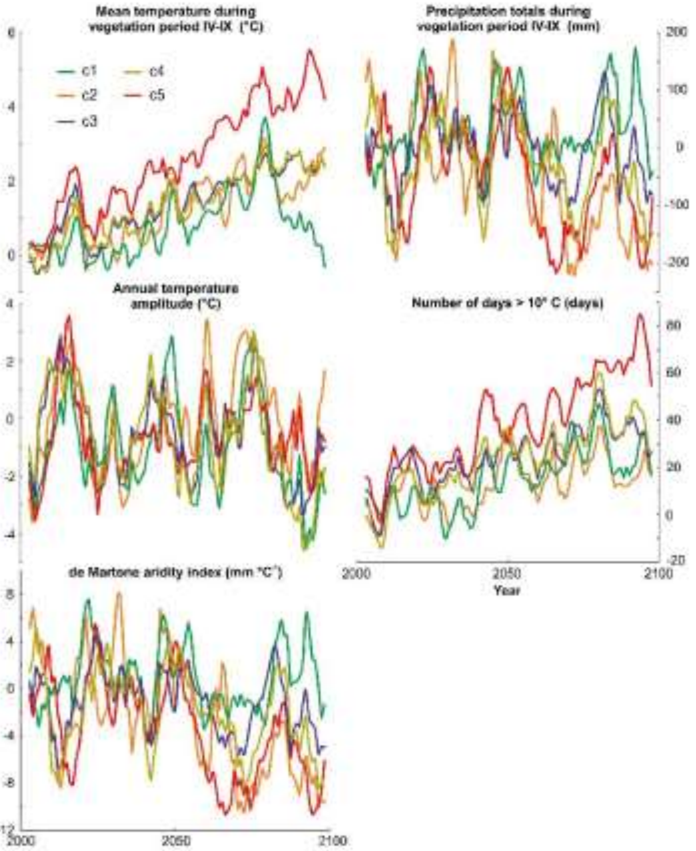

Fig. A1 Climatic drivers of forest development in the forest dynamics model Sibyla and their development to the year 2100 according to five climate change scenarios. Changes between the projections based on 5 GCM-RCM couplings and stable climate referring to the period 1981-2010.

SUPPLEMENTARY MATERIAL B: MEMBERS OF THE REGIONAL STAKEHOLDER PANEL

Tab. B1 Members of the Regional Stakeholder Panel

Sector	**Stakeholder type**	**Stakeholder detail**
Forestry	local	Forest owner
	local	Head of forest enterprise
	local	Forest manager (responsible for silviculture)
	local	Forest manager (responsible for harvesting)
	local	Licensed forester
	regional	Regional Forest Office in the Prešov city
Other	local	Slovak Fishing Association – Local organization Poprad
	local	Cycling Sport Club „HORAL"
	local	Hunting Association „Bor Spišská Teplica"
	local	Tourism Club "Spišské Bystré"
	International	Forest Stewardship Council
	national	Administration of the National Park „Slovak Paradise"
	local	Village Mayor of the Spišské Bystré municipality
	local	Village Mayor of Spišská Teplica municipality

SUPPLEMENTARY MATERIAL C: DETAILED DESCRIPTION OF THE INVESTIGATED MANAGEMENT SYSTEMS

Management system	**NM**	**FM**	**BAU**	**OSH**
Management type	—	Rotation	Rotation	Continuous cover
Silvicultural system	—	Shelterwood	Shelterwood	Shelterwood to selective
Target age structure	All-aged	Even-aged	Even-aged	All-aged
Rotation period	—	90 years	100 years	>120
Final cutting area	—	< 3.00 ha	< 3.00 ha	< 0.02 ha
No. of harvest operations in a cutting area within a stand[*]	—	1 – 2	2 – 3	> 3
No. of harvest operations in the whole stand[**]	—	3 – 4	4 – 6	> 6
Regeneration period of the whole stand	—	20 - 30 years	30 - 40 years	from 50 years to steady
Natural regeneration	++	++	+	+
Artificial regeneration (planting)	--	+	++	+
Planted tree species[***] (ranges between the 25 simulated forest stands are indicated)	—	Spruce 70% Fir 0-15% Larch 0-15% Maple 0-30% Beech 0-15%	Beech 10-30% Larch 0-20% Fir 10-20% Pine 0-20%	Beech 20-40% Fir 20-40% Spruce 0-30% Maple 0-30%
Thinning method	—	from bellow	neutral	from above
Frequency of thinning		3-4 / 10-20 year step	3-4 / 15-20 year step	3 / 15 year step
Stakeholder preference	—	high income, low costs, reduced risk of damage	wood production balanced with other ecosystem services	no visible cuts, continuous cover, naturalness
Importance of wood production	--	++	+	-
Importance of biodiversity	++	--	+	+
Importance of social values	+	--	-	++

[*] Harvest operations are applied in several parallel strips in each stand. We refer to a single strip as a "cut area"

[**] Number of harvest operation in the whole stand roughly equals to the number of operation in a cut area × the number of strips; the difference might arise when two strips are harvested at the same time

[***] Planting is applied after the final harvest operation in each cut area. Tree species percentage in the planting is indicated.

Importance level: ++ very important, + important, - less important, - - unimportant, — irrelevant for given management system

Management systems: NM – no-management; BAU – business-as-usual, i.e. the currently applied management; FM – management based on the preferences of forest managers; OSH – management based on preferences of other regional stakeholders

NM – no management

No management operations are applied. In case for the Net Present Value calculation, a variant of NM, which contains the removal of dead trees, is also tested ($NM_{salvage}$).

FM – management system preferred by the regional forest managers

System of intensive spruce oriented silviculture. FM reflected the desire of forest managers to produce softwood timber and to reduce planting costs. Regular thinning from bellow with intensities according to the decennial thinning percentage (Halaj et al. 1986) dependent on tree species, site index, stand age and stocking is applied. Natural regeneration of spruce is supported by the two-phase shelter cuts. Planting is applied when the natural regeneration fails. Rotation period is shorter that in BAU to reduce the risk of stand failure. Artificial regeneration (planting) is protected by regular weeding and against game browsing (these operations affect management costs).

BAU – currently applied management system

System based on the current Slovak forestry legislation that supports the multifunctional use of forests. Regular neutral thinning with intensities specified by the decennial thinning percentage (Halaj et al. 1986) and support to the admixed tree species are applied. Rotation and regeneration periods are applied according to the national forestry regulations (Forest Management Models). Natural regeneration of spruce is combined with planting of other target tree species in proportions specified in Table C1.

For planting (i.e. artificial regeneration), regular weeding and protection against game browsing is applied. Tending operations are applied for all established young stands, differentiated by site units, tree species and silvicultural system.

OSH – management system preferred by forest managers

System oriented on the transformation of even-aged forest to close-to-nature uneven aged (selection) forest. OSH attempts to support biodiversity (including by planting), forest aesthetic value and promotes long rotation periods and small-scale interventions. Intensive thinning from above with intensities twice higher as compared to the decennial thinning percentage (Halaj et al. 1986) is applied to support admixed tree species, diversity and vertical differentiation of the stands.

Rotation and regeneration periods are significantly prolonged as compared with the BAU. More frequent and less intensive final cuts are applied. Natural regeneration of spruce is combined with planting of desired tree species (Table C1). Density of natural regeneration for each tree species is evaluated in the year of the prescribed planting. If the density is lower than expected, planting is applied. Protection of planted trees as well as newly established young stands were implemented as in the case of the BAU management.

SUPPLEMENTARY MATERIAL D: DETAILED INFORMATION ON THE CALCULATION OF NET PRESENT VALUE

The NPV calculation

The net present value (NPV) was calculated as sum of discounted net cash flows. The interest rate was 2%. The NPV was calculated for each simulated stand separately. The € ha^{-1} units weighted by stand area of each stand were used for the final evaluation. A net cash flow for each year of the simulation period was calculated as the timber price from sold timber minus harvest costs, both in m^{-3} and weighted with timber volume. In case of stands that were newly established after harvests or calamities or of young stands, net cash flows were reduced by silvicultural costs in € ha^{-1}. The net cash flows were calculated in a time step of 5 years. Each net cash flow was discounted to the starting year of simulation in 2010. While the model Sibyla allows to calculate the thinning and final cut related costs and revenues only, the silvicultural costs that incurred up to the last tending had to be evaluated separately.

To compare the tested management alternatives, the value of the remaining stand at the beginning and at the end of the simulation period was considered.

Timber prices

Timber prices were evaluated using a simplified approach that uses three price classes for each tree species only: sawlog (assortment classes I, II and III according to Petráš et al. 1996), pulpwood (assortment class V) and fuelwood (assortment class VI) (Tab. D1). The prices were collected from the investigated forest enterprise to be specific for the regional conditions.

Tab. D1 Prices of tree species and assortments used in the calculation of the net present value generated by the tested management systems

Species	Assortment	Avg. price [€ m^{-3}]
Spruce	Sawlog	66
	Pulpwood	35
	Fuelwood	20
Pine	Sawlog	56
	Pulpwood	31
	Fuelwood	18
Fir	Sawlog	65
	Pulpwood	35
	Fuelwood	20
Beech	Sawlog	48
	Pulpwood	38
	Fuelwood	37
Oak	Sawlog	59
	Pulpwood	35
	Fuelwood	34

Harvesting costs

Working cost per hour, material consumption for cutting and yarding, taxes and compensation were considered (Tab. D2). The harvest costs are differentiated by method of harvesting (tree, stem, log), tree class (structure of stem and branches in degrees from 1 to 3) and volume of the intermediate stem specific for each stand. Additional harvest costs can be induced by unfavourable working conditions and yarding distances. To consider such effects, data from Slovak technical norms were used to define the respective coefficients. While Tab. D2 shows rather detail breakdown of harvest costs used in the Sibyla model, an aggregate harvest costs per m^3 are given in Tab. D3.

Tab. D2 Detail costs of the evaluated management operations

Material consumption		
Forest tractor	€ m$^{3\ -1}$	2.15
Chainsaw	€ WH^{-1*}	1.2
Wage tariff		
Cutting	€ h^{-1}	5
Yarding	€ h^{-1}	5
Conversion	€ h^{-1}	5
Other indices		
Compensations**	%	130
Wage taxation***	%	38

* WH Working Hour

**coefficient of compensation for the chain-saw (cutting, wood conversion), multiplied by material costs per man-hour and volume

***wage cost is calculated from wage taxation multiplied with final man time and volume

Tab. D3 Costs of harvesting operations used to calculate the net present value for the tested management systems

Stand age	**Standing**				**Regular cutting**				**Salvage cutting**			
	NM	BAU	FM	OSH	NM	BAU	FM	OSH	NM	BAU	FM	OSH
20	30.64	30.64	30.64	30.64								
30	32.35	32.33	32.34	30.83			31.81	31.51	21.60	22.54	21.60	21.97
40	28.72	28.73	28.44	25.94			32.64	35.10	39.27	40.08	37.20	35.86
50	17.52	17.12	16.70	15.04				19.58	29.78	29.70	29.17	24.19
60	13.73	13.76	13.20	11.83			32.59	28.13	23.05	22.29	22.87	18.15
70	12.24	12.43	12.00	11.24					18.48	19.93	18.46	16.38
80	10.99	11.09	10.67	10.53		8.92	5.88	12.07	16.63	16.58	16.41	14.89
90	10.22	10.43	10.01	9.86		9.48	9.88	9.43	15.05	14.77	14.92	14.23
100	9.87	10.08	9.62	10.00		9.69	9.35	8.82	14.19	14.21	13.98	13.69
110	9.53	10.00	9.96	9.60		9.25	8.88	8.77	13.56	13.75	13.33	13.79
120	9.21	10.10	9.65	9.87		8.76	8.78	8.42	12.81	12.95	13.20	12.87

Tab. D4 Mean harvest costs in € m^{-3} specific to forest management type and stand age category. Average of all model stands is presented.

Stand age	Harvest cost of the remaining stand in year 2010 and 2100				Regular cutting				Salvage cutting			
	NM	BAU	FM	OSH	NM	BAU	FM	OSH	NM	BAU	FM	OSH
20	35.50	35.50	35.50	35.50	–	–	–	–	36.27	36.38	36.27	36.38
30	38.05	38.05	38.07	38.25	–	–	35.40	36.71	34.70	34.94	34.91	34.91
40	41.25	41.25	41.41	42.22	–	–	39.04	38.71	35.77	35.90	35.72	35.71
50	55.39	55.46	55.86	56.53	–	–	–	49.77	39.98	39.47	39.84	40.59
60	58.56	58.63	59.15	59.73	–	–	41.24	41.93	41.65	41.84	41.74	42.67
70	60.24	60.30	60.82	60.89	–	–	–	–	43.27	43.08	43.27	43.98
80	61.42	61.40	61.88	61.73	–	62.63	64.25	58.30	43.80	43.57	43.81	44.09
90	62.01	61.89	62.39	62.18	–	62.81	62.98	62.66	43.85	44.20	44.10	44.20
100	62.31	62.04	62.56	62.33	–	62.70	63.10	63.31	44.25	44.11	44.32	44.46
110	62.60	62.35	62.69	62.58	–	62.55	63.42	62.89	44.55	44.67	44.94	44.22
120	62.92	62.09	62.31	62.50	–	62.94	63.26	63.40	44.42	44.77	44.38	44.94

Silvicultural costs

Silvicultural costs include area cleaning, soil preparation, afforestation, fencing (in case of clearcut), tree protection, weed and sprout removal (in case of clearcut) and tending. Silvicultural costs are specific for site and management type (clearcut, shelterwood).

Number, timing and intensity of tending, thinning and final cut were dependent on tested management system and site index. For the "no management" alternative, no silvicultural costs were considered.

Tab. D5 Mean silvicultural costs (planting, tending) € ha^{-1} specific to forest management and stand age category

Age class	BAU	FM	OSH
0	1203	1057	689
5	131	550	494
10	865	711	310
15	364	239	372
20	337	78	484
25	34	6	174
30	0	0	18
Undiscounted Sum	2935	2641	2540
Discounted Sum (2 %)	2550	2372	2108

Effect of forest damages on NPV

Additionally to tree inherent mortality, the effect of disturbances was considered in forest development simulations. Parameterization of the disturbance module was described in Hlásny et al. (2015). Disturbances can affect the timber price directly through the compromised timber quality and indirectly through the increased harvesting costs and premature felling of trees. While biotic damage (mainly infestation by bark beetle *Ips typographus* in the study region) can have an adverse effect mainly through the premature felling of trees, abiotic damage, such as wind and snow, can compromise the timber quality substantially. We used the national statistics on forest damage (National Forest Centre Slovakia, internal data) to assess the long-term ratio of biotic and abiotic damage in the study region as well as to assess the approximate coefficients that could be applicable for reducing the price of sanitary harvested wood and increasing the harvesting costs (Tab. D6). Because 94 % of trees damaged by disturbances in the model regions are spruces, we applied such a correction for spruce only. Effect of damage on timber price of the remaining species was considered as negligible.

Tab. D6 Coefficients used to modify the net present value calculation due to damage to spruce

Damage	Share of sanitary felling	Timber price reduction	Harvesting cost increase*
Abiotic	40 %	15 € per cubic meter of saw-wood	1.5
Biotic	60 %	15 € per cubic meter of saw-wood	1.3

*Multiplication of the harvesting cost of undamaged wood

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5.8 Climate change increases the drought risk in Central European forests: What are the options for adaptation?

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PÔVODNÁ PRÁCA – ORIGINAL PAPER

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Climate change increases the drought risk in Central European forests: What are the options for adaptation?

Klimatická zmena zvyšuje riziko sucha v stredoeurópskych lesoch:
Aké sú možnosti adaptácie?

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Abstract

The paper presents information on the projected drought exposure of Central Europe, describes the anticipated dynamics of the regional forests, and identifies measures facilitating the adaptation of forests to climate change-induced drought risk. On the basis of an ensemble of climate change scenarios we expect substantial drying in southern Slovakia and Hungary, while such trends were found to be less pronounced for the Czech Republic and Austria. In response to these climate trajectories, a change in species composition towards a higher share of drought tolerant species as well as the use of drought resistant provenances are identified as paramount actions in forest adaptation in the region. Adaptation to aggravating climate change may need to use artificial regeneration to enrich local gene pools and increase the drought tolerance of stands. Increasing risks from pests, pathogens and other disturbances are expected as a result of more frequent and severe droughts, underlining the need to put a stronger focus on risk management principles rather than on indicators of productivity in silviculture and forest planning. A consolidation of disturbance monitoring systems and a broader use of pest dynamics and hazard rating models are paramount tools to facilitate this adaptation process in forest management. The effectiveness of all the suggested measures needs to be controlled by efficient forest monitoring systems, the consolidation of which seems to be a timely task. Systematic and long-term implementation of the presented measures should increase forest stability and resilience, and further secure the sustainable provision of ecosystem services under climate change.

Key words: drought stress; temperate forests; adaptation measures; species shift; forest disturbances

Abstrakt

V článku sú prezentované informácie o očakávanom vývoji sucha v oblasti strednej Európy, je opísaná možná dynamika lesov v podmienkach zmeny klímy, a je vypracovaný systém opatrení umožňujúcich adaptáciu lesov na zmenu klímy. Na základe kolekcie scenárov zmeny klímy bol identifikovaný výrazný nárast intenzity sucha v oblastiach južného Slovenska a Maďarska, zatiaľ čo v oblasti Českej republiky a Rakúska bola zmena relatívne nevýrazná. S ohľadom na tento vývoj predstavuje úprava drevinového zloženia smerom k vyššiemu zastúpeniu sucho tolerujúcich drevín a širšiemu využívaniu proveniencií rezistentných voči suchu jedno zo základných adaptačných opatrení. V prípade výrazných zmien klímy narastá význam umelej obnovy, ktorá predstavuje nástroj na zlepšovanie druhovej a genetickej diverzity porastov a zvyšovanie ich tolerancie voči suchu. Narastajúci vplyv škodcov súvisiaci s rastúcim vplyvom sucha a ďalších abiotických činiteľov naznačuje potrebu orientovať pestovanie a hospodársku úpravu lesa viac na manažment rizík ako na maximalizáciu produkcie. Konsolidácia systémov monitoringu škodlivých činiteľov a širšie využívanie modelov dynamiky škodcov a hodnotenia rizík patria medzi ďalšie dôležité opatrenia podporujúce adaptáciu lesov na zmenu klímy. Všetky uvedené opatrenia musia byť podporené informáciami získanými na základe dlhodobého monitoringu lesa, ktorý však vyžaduje urýchlenú konsolidáciu. Systematická a dlhodobá realizácia prezentovaných opatrení podporí stabilitu a rezilienciu lesov a vytvorí predpoklady pre udržateľné poskytovanie ekosystémových služieb a funkcií v podmienkach zmeny klímy.

Kľúčové slová: stres suchom; lesy mierneho pásma; adaptačné opatrenia; posun druhov; rozvratné činitele lesa

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1. Introduction

Climate change is expected to have a profound effect on Central European forests (Tatarinov & Cienciala 2009; Hlásny et al. 2011a, b), although this region has not received adequate attention in climate change research and adaptation thus far. Central Europe belongs to the temperate oceanic and temperate continental bioclimatic zones (Rivas-Martinez et al. 2004), where drought, storms and related changes in biotic disturbance regimes are expected to be the main climate change related impacts (Bréda et al. 2006; Lindner et al. 2010). Research of drought effects on temperate forest ecosystems identified a range of possible responses, including a change in forest production and carbon accumulation (Ciais

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*Corresponding author. Tomáš Hlásny, e-mail: hlasny@nlcsk.org, phone: +421 45 531 41 75 et al. 2005; Tatarinov & Cienciala 2009), a shift in species competitive capacity with potential risks to species and genetic diversity (Archaux & Wolters 2006; Borovics & Mátyás 2013; Cavin et al. 2013; Mette et al. 2013), drought induced forest dieback (Jump et al. 2009), as well as an increase in susceptibility to biotic disturbance agents (Desprez-Loustau et al. 2006; Rouault et al. 2006). In addition to increasing the susceptibility of trees, growing virulence of antagonists and an escalating number of newly invading pests have been observed (Csóka & Hirka 2011). Forest fires in regions where this agent has been of minor importance historically represent another potential threat to Central European forests (e.g. Reinhard et al. 2005). Although observations of critical drought effect in Central Europe have been relatively rare until now, effects such as drought-induced decline of tree species (Siwecki & Ufnalski 1998; Mátyás et al. 2010a) or changes in population dynamics of climate sensitive pests (Hlásny & Turčáni 2009; Lakatos & Molnár 2009) have already been reported. Furthermore, observations around the globe, such as climatically induced decline of diverse Abies and Pinus species in the temperate forests of North America (van Mantgem & Stepheson 2007) are also deemed possible for the future in Central Europe.

In addition to ecological impacts, the substantial economic losses expected in relation to climate change (Hanewinkel et al. 2012) may adversely affect regional economies, including impacts on rural communities. Apart from direct impact on timber production, the quality of non-productive forest services might also be compromised by a changing climate (Briner et al. 2013). Therefore, development of appropriate forest adaptation measures, their inclusion into national legislation, and implementation to practical forest management are urgently needed. A growing body of literature on forest adaptation points to possible actions as well as barriers to the implementation of adaptation measures in forestry (Spittlehouse & Stewart 2003; Bolte et al. 2009; Lindner et al. 2010; Kolström et al. 2011). Such measures need to be regionally adapted to address the regional climatic exposure and sensitivity of ecosystems, as well as to account for the current ecological and socio-economic conditions (Lindner et al. 2010). In this paper, we strive to provide essential information on the anticipated drought risks in Central European forests, and recommend forest adaptation measures specific to this region. In particular, our objectives are:

- to evaluate the projected climatic exposure of Central Europe with regard to drought;
- to review anticipated drought-related risks to Central European forests; and
- to compile possible adaptation measures to deal with drought-related climate change impacts in Central European forests.

2. Data and methods

2.1. Region of interest

We selected a rectangular area covering the entire Slovakia, Czech Republic and Hungary, as well as parts of Austria, Germany, Poland, Ukraine, Croatia, Slovenia, Italy, Serbia, and Romania as our study region, covering a total of 491,000 km^2 (Fig. 1). Forests cover 32% of the study region (Corine LandCover 2000, EEA 2006). The region encompasses a substantial climatic gradient, with diverse forest communities and land uses from the semiarid plains of Hungary to the highest peaks of the Carpathians and the Eastern Alps. Climatic continentality is increasing across the region from the West towards the East. The Southwest is under a sub-Mediterranean influence. A specific feature of the region is that most dominant, zonal tree species reach their low-elevation (xeric) distributional limits here. Therefore, increasing drought is important limiting factor and future threat to forests in this region.

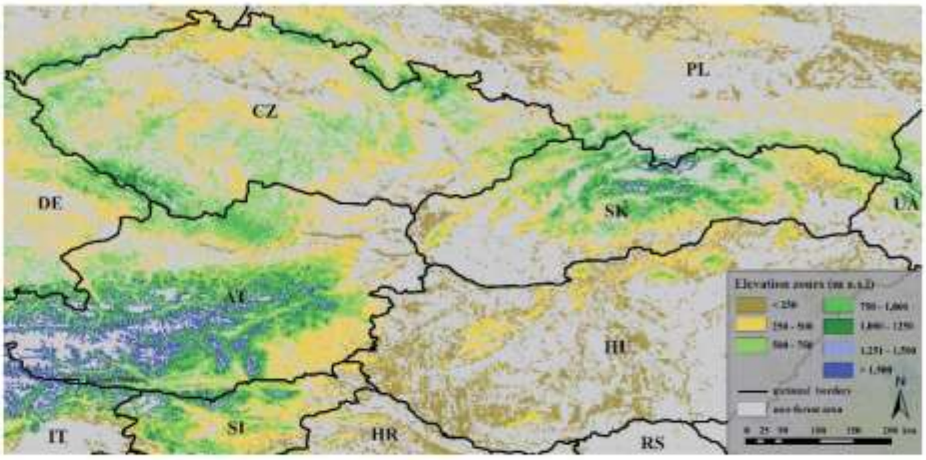

Fig. 1. Forests of the study region classified by elevation zones.

The projected climatic exposure will be evaluated for the entire study region, while forest adaptation measures will primarily address the northern part, i.e. northern Hungary, the Czech Republic, Slovakia and Austria. This sub-region contains a gradient of zonal forests dominated by *Quercus* sp., *Fagus sylvatica*, *Abies alba* and *Picea abies*, with azonal occurrences of *Pinus sylvestris*.

2.2. Climate data – The FORESEE database

The FORESEE climatic database was developed to support climate change related research in Central Europe, and to ease the access to climate data (Dobor et al. 2013; http://nimbus.elte.hu/FORESEE). The database contains gridded daily observational data (1951–2009) based on the E-OBS and CRU TS datasets (Mitchell et al. 2004; Haylock et al. 2008), and an ensemble of climate projections (2010–2100). The future climate is represented by bias corrected meteorological data from 10 regional climate models (RCMs), driven by the A1B emission scenario (Source: the ENSEMBLES database, van der Linden et al. 2009). The database contains daily air temperature and precipitation data as well as numerous climate indices. The original ENSEMBLES and E-OBS data were interpolated to a uniform 1/6×1/6 degree horizontal resolution grid.

2.3. Assessment of the regional climatic exposure with respect to drought

To evaluate the climatic exposure of the study region, we produced high resolution (250×250 m) climatic maps for two time periods – 1961–1990 (reference period) and 2071–2100 (future period); the future climate data were calculated as the average of the 10 RCMs included in the FORESEE database. Kriging with External Drift, a spatial interpolation method which was previously found suitable for the interpolation of climate data, was used to derive the climatic maps (Hudson & Wackernagel 1994; Vizi et al. 2011). A digital elevation model with a spatial resolution of 250 metres was used to support the interpolation. The climatic exposure was calculated as the difference in climate between periods 1961–1990 and 2071–2100. As drought is of prime interest in the current study, we evaluated the change in precipitation totals during growing season (April–September) as well as in the Ellenberg climatic quotient. The Ellenberg climate quotient (EQ) expresses the coupled effect of temperature and precipitation. It is defined as the ratio of the mean air temperature of the long-term warmest month (MTWM) to the annual precipitation sum (AP):

$$EQ = MTWM / AP \times 1000$$

This quotient has been repeatedly used, for example to separate the areas dominated by beech from areas of boreal or thermophilic species (e.g. Jensen et al. 2004; Fang & Lechowicz 2006), as well as to evaluate anticipated changes in the beech distributional range (Mátyás et al. 2010a).

2.4. Proposed adaptation measures

We reviewed a body of literature to compile a list of possible adaptation measures and, where necessary, adopted measures reported in the literature to the specific conditions of Central Europe. The proposed measures address all aspects of forest management, and focus mainly on commercial and protective forests. Protected forests, with the main aim of conserving biodiversity, were not in the focus of this study. As we mainly address drought-related processes, some beneficial effects of climate change, which might be pronounced in mountain regions (e.g. Bergh & Linder 1999; Seidl et al. 2011a), and which thus present opportunities for forest management, have not been addressed here either. Hence, the suggested measures primarily concern lowland forests (except for floodplains), and zonal forests in the foothills and medium altitudes, except where stated otherwise.

3. Results and discussion

3.1. Future drought exposure of Central Europe

The pattern emerging for the study region is a decreasing gradient of growing-season precipitation from the North-West to the South-East (Annex 1). While projected precipitation remains more or less stable in the Czech Republic and Austria (i.e. comparable with the period 1961–1990), a decrease is projected for the entire area of Slovakia and Hungary. Though the decrease is moderate in absolute terms, ranging from –50 to –100 mm, it indicates a substantial drying of climate in southern Slovakia and throughout Hungary. When expressed in relative terms, these changes amount to reductions of up to 25% for southern Hungary, with most of Slovakia experiencing reductions by 10%. In the Czech Republic and Austria changes mostly remain within ±5% of the reference period. For Hungary and southern Slovakia, projections also indicate an increase in the frequency of consecutive drought extremes, which may be especially threatening to less drought tolerant species (Gálos et al. 2007).

The described precipitation change occurs concurrently with the increase in air temperature, which strengthens the atmospheric evaporative demand and thus amplifies the potential water deficit of plants. A multimodel projection of the mean annual air temperature indicates an increase ranging from ca. 1.4 °C in the North-West to 2.0 °C in the South-East of the region in the first half of the century, and an increase from ca. 3.1 °C to 3.8 °C by the end of the century (not presented in the Annexes).

The amplifying interaction between temperature and precipitation is captured by the Ellenberg climate quotient (Annex 2). While the main forested areas of Slovakia and the Czech Republic were in the range of Ellenberg quotient between 5 and 30 under the reference climate, future projections imply a potential decrease in water availability to plants over large areas by the end of the century (Annex 2). Critical drying of climate was projected to occur in Hungary, where values of up to 50 were projected across most of the country. It is noteworthy that value of 29 represents the approximate limit of distribution for European beech-dominated forest types, while values above 40 have been associated with beech decline (Fang & Lechovicz 2006; Mátyás et al. 2010a). The difference map shows gradient of climatic drying from the North-West to the South-East of our study region. An increase in the Ellenberg quotient by up to 4 units is projected to occur in most of the uplands and mountain areas of the Czech Republic and Austria, while large areas of southern and eastern Slovakia are projected to face an increase by 4–10 units. The increase in large parts of Hungary was projected to be in the range 10–16 units. Thus the projected future conditions could represent critical conditions for the persistence of drought-sensitive species: For example, Mátyás et al. (2010a) suggested that beech forests may experience large-scale mortality if the Ellenberg quotient increases by more than 13 units compared to the long-term average.

3.2. Anticipated forest dynamics under climate change as a starting point for adaptation

We here address the anticipated response of three main Central European zonal tree species or species groups, i.e. oaks (*Quercus* sp.), European beech (*Fagus sylvatica*), and Norway spruce (*Picea abies*). These species constitute 71% of forest in Slovakia, 66% in the Czech Republic, 72% in Austria, and 42% in Hungary.

3.2.1. Succession, colonisation and retreat

Oaks are known to be able to maintain their physiological performance under heat and drought (Dickson & Tomlinson 1996; Gallé et al. 2007), although inter-species differences are large (e.g. Acherar & Rambar 1992). Their drought resistance along with their low biotic and mechanical vulnerability implies that oak species might be increasingly successful under climate change in Central Europe. Climatic envelopes suitable for oaks were projected to expand substantially to higher elevations and latitudes (Peñuelas & Boada 2003; Hanewinkel et al. 2012). Hanewinkel et al. (2012) suggested that climates suitable for Mediterranean-type oaks may cover substantial proportions of Slovakia, Austria, the Czech Republic and all of Hungary by the end of the Century. In contrast, the area with climate conditions suitable for the present oak species is projected to shrink. Hlásny et al. (2011a) found, on the basis of growth simulations, that production of oaks could remain stable under climate change in the current distributional range of oaks in Slovakia, and climates suitable for oaks may extend to elevations up to 1,000 m a.s.l. Also in Austria, oaks are expected to substantially increase in their competitive strength and expand their range into the mountainous parts of the country (Lexer et al. 2002). Such facts support the potential importance of oak species under drier and warmer climates in Central Europe. Despite numerous evidence on the positive effects of climate change on oaks, and the proven capacity of oaks to sustain prolonged droughts, oak mortality following severe drought episodes was repeatedly observed in many European countries (Delatour 1983; Archaux & Wolters 2006; Massarutto et al. 2013). Such processes may result in loss of competitive strength and retreat of distribution in some oak species, as has been predicted, for instance, for sessile oak (*Q. petraea*) in Hungary (Czúcz et al. 2011).

As climate change may force a natural replacement of European beech by oaks in certain regions, the difference in climatic sensitivity between these two species can substantially shape the future of some European forests (Czúcz et al. 2011; Scharnweber et al. 2011). The climate sensitivity of European beech has recently been investigated by various authors (Leuzinger et al. 2005; Geßler et al. 2007; Mátyás et al. 2010a; Czúcz et al. 2011), suggesting the potential for decline of large proportions of current beech forests in the future. For example, extreme drought between 2000 and 2003 induced a decline of beech vitality accompanied by biotic damage, followed by large scale beech mortality in Hungary and Eastern Slovenia (Lakatos & Molnár 2009; Mátyás et al., 2010a). Growth simulations performed in Slovakia imply that beech production may decline in Central Europe up to elevations of ca. 500 m a.s.l. by the end of the century. Specifically, mortality may occur in up to 5% of current beech stands in the country, and 70% of stands lie in the area of declining production (Hlásny et al. 2011a). In areas of better water supply as well as in mid- to high elevation areas of the Eastern Alps beech has been reported to primarily respond positively to climatic changes (Seidl et al. 2008a; Seidl et al. 2011a). Yet, in low elevation areas potential increases in beech defoliation by gypsy moth (*Lymantria dispar*) (Csóka & Hirka 2006; Hlásny & Turčáni 2009) as well as potential damage by beech bark beetle (*Taphrorychus bicolor*) (Lakatos & Molnár 2009) may further reduce the vitality of trees and support the expansion of oaks and other drought tolerant species.

Norway spruce has widely been planted in Central Europe at lower elevations for centuries, resulting in much higher shares of the species than its natural proportion (Ellenberg 1963; Spiecker et al. 2004; Hlásny & Sitková 2010). The current spruce shares are 26% in Slovakia, 52% in the Czech Republic, 60% in Austria and 1.5% in Hungary. Most of these forests are man-made and distributed largely outside the range of spruce natural distribution; these forests are prone to an array of pests and diseases, and outbreaks can be triggered by relatively minor climatic or other stressors (Seidl et al. 2008b; Wermelinger 2004). Progressive drought may adversely affect the species both directly as well as through an increase in biotic damages, especially at low to mid elevations, which may cause substantial forest decline over large areas (Hlásny & Turčáni 2013). Extensive decline of spruce forests may accelerate the expansion of broadleaved species, mainly of beech and pioneer tree species. The decline of secondary spruce forests may be accelerated in many regions by an increase in the number of bark beetle generations developed per year (Seidl et al. 2008b; Hlásny et al. 2011c) as well as by the influx of new pests, such as *Ips duplicatus* (Holuša et al. 2013). Thereby, spruce forests may be the most dynamically changing forest type in Central Europe under climate change.

3.2.2. Within-species genetic adaptation processes and their potential for adaptive forestry

Climate change forces the ecosystem to adapt at different levels – in species composition as well as at genetic level through selective pressure. Adaptation in the strict sense can be defined as the genetic adjustment of a population to actual abiotic and biotic environmental factors, leading to shifts in frequencies of gene variants (alleles) (Borovics & Mátyás 2013). Selective forces in different environments lead to diverse adaptive optima. This implies that differently adapted populations exist in all forest tree species of wide distribution, depending on local site and climate conditions.

Adaptive genetic variation created by natural selection provides an important option supporting the adaptation of trees to changing climates. It is assumed that populations growing in conditions analogous with expected future climates may better fulfill the expectations with regard to stability and growth performance. Provenance tests provide sufficient information about the response of progenies raised from reproductive material of non-local origin transferred into new environments, differing from their original habitat (Mátyás 1994). A common experience of these tests is the stability of performance across considerably changing climates. If the environmental change exceeds the level of genetically determined tolerance and stability, vitality starts to decline exponentially, finally leading to death and extinction (Mátyás et al. 2010b). The degree of stability[1], i.e. the ability of populations to maintain productivity across changing conditions is inherited and may vary within species. For instance, Norway spruce populations from the Eastern Carpathians were found to perform better under changing environments than others. These stable (plastic) populations should be identified and preferred for artificial regeneration, as they are more tolerant and resilient to new environments (Mátyás & Borovics 2014).

3.3. Proposed adaptation measures

3.3.1. Change of tree species composition

Changing the prevailing tree species composition in response to increasing drought is a paramount measure in adapting forest ecosystems to climate change. The measure is primarily aimed at increasing the share of drought tolerant species, reduction of water demanding and drought vulnerable species, increasing stand diversity (which supports the inherent adaptive capacity of forests), and reducing the share of host trees within the outbreak range of biotic disturbance agents. The importance of such measures increase towards the lower range (xeric) limits of species, where adverse effects of drought might be more pronounced (Jump et al. 2009). It has to be noted, however, that such measures are associated with considerable lead times and will only gradually become effective (see e.g., Seidl et al. 2009), which underlines the importance for timely and anticipatory adaptation actions in forestry.

Adaptation potential of oak species

A continuous increase of the share of oak species to the detriment of beech and some coniferous species in lower to medium elevations is a measure of high importance. In drought exposed sites, oaks that are currently at their northern distributional limit in Central Europe, such as *Q. cerris* – or even rare species such as *Q. pubescens* and *Q. frainetto* – appear to be sound options to adjust current species composition. An enrichment of the current beech-dominated forests by oaks should also be considered in the mid-elevation range (400–800 m a.s.l.). The share of *Q. petraea* and *Q. robur* could be increased in *some intra*-mountain valleys. Q. robur, which was found sensitive to ground water depletion (Friedrichs et al. 2009), should be used cautiously. Hornbeam-oak communities with conifers, containing *Carpinus betulus, Q. robur, Abies alba*, and *Picea abies*, which are considered native in some intra-mountain valleys in Slovakia (Michalko 1980), could in the future be used also on the adjacent slopes and higher elevations as well as in other regions in Central Europe. On some slopes, *Q. petraea* may replace *Q. robur*, and form mixed stands with beech and drought tolerant conifers such as *Pinus sylvestris* and *Larix decidua*. In the Eastern Alps of Austria, for instance, increasing the share of oak on selected sites was found to considerably lower the risk of bark beetle damage and reduce overall climate change vulnerability of forests (Seidl et al. 2008b; Seidl et al. 2011b).

Risks and opportunities of using European beech in forest adaptation

Although the proportions of European beech in Central European forests vary among countries (Slovakia 31%, Czech Republic 7%, Austria 9.5%, Hungary 7%), the role of this species in forest adaptation seems indispensable (Tarp et al. 2000; Spiecker et al. 2004). In the future, current beech forests are expected to persist mainly in higher elevations (ca. above 800 m a.s.l.), and expand respectively. In some regions, beech is expected to be used as important surrogate species in the reconstruction of vulnerable spruce-dominated forests (e.g. Spiecker et al. 2004; Seidl et al. 2008b). The projected shift of the beech production optimum to elevations around 1,200 m a.s.l. (Hlásny et al. 2011a) by the end of the century implies that beech will be a key species for future forest management in mountainous regions. However, the climatic sensitivity of beech suggests the need of reducing the extent of present lower-elevation beech forests in Central Europe, and increase their diversity to lower climate vulnerability and risk. As the Ellenberg climatic quotient was found to be a powerful predictor of the distribution and vigour of beech (Fang & Lechowicz 2006; Mátyás et al. 2010a), the climate projections presented in the current study (Annex 2) can be used to identify the areas where beech is expected to suffer from drought in the future, and where more drought tolerant species should be introduced. While the need of such interventions seems marginal in the Czech Republic and Austria, it will be increasingly necessary in southern Slovakia and Hungary.

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[1] stability of performance is quite often (in a strict sense, falsely) described as "phenotypic plasticity". Stability or "plasticity" describes the extent to which growth and vitality of a population is maintained across a range of environments relative to other, e.g. local populations. Stability itself is also a genetically determined trait.

Adjustment of species composition in secondary Norway spruce forests

A measure of paramount importance is the reduction of secondary spruce forests at elevations below ca. 800 m a.s.l., and their conversion to mixed and broadleaved forest types. This measure supports climate change adaptation, although the main driver of the currently ongoing conversion efforts are already observed extensive diebacks of spruce forests (Uniyal & Uniyal 2009; Hlásny & Sitková 2010; Hlásny & Turčáni 2013). The assessment of the urgency of conversion should strictly follow risk assessment principles (Netherer & Nopp-Mayr 2005; Kulla & Marušák 2011).

However, spruce will also retain a major role in Central European forests in the future as it can be particularly beneficial for biodiversity, stability and timber production as admixed species. The latter is particularly the case in higher elevation mountain forests, where longer vegetation periods are expected to result in improved growing conditions for spruce (Seidl et al. 2011a). Enrichment of spruce stands by broadleaves was found to significantly increase a probability that the stand reaches maturity, although the economic aspects of such interventions have not yet been sufficiently explored (Griess & Knoke 2013; Roessiger et al. 2013).

Supporting biodiversity using enrichment species

In addition to the three main species discussed above there are number of species which may be used to enhance the diversity and drought tolerance of current forests. The proportion of species with climatic tolerance similar to oaks, such as *Fraxinus ornus, Acer campestre, Sorbus torminalis, Tilia cordata* and *T. argentea* could be increased in low to mid elevation beech and spruce forests. The share of these species can also be expected to increase spontaneously in response to climate drying. Scotch pine (*Pinus sylvestris*), European larch (*Larix decidua*) and even introduced conifers, such as Douglas fir (*Pseudotsuga menziesii*), could also be used as suitable enrichments in medium to higher elevation forests.

Species translocation, assisted migration and introduction

The anticipated increase in forest dynamics in Central Europe owing to climate change driven disturbances and potential species shifts suggest the need for non-traditional approaches supporting the change in tree species composition. Although the concept of assisted colonisation (Svenning et al. 2009) was originally intended as a proactive conservation strategy, it also seems to be effective as an adaptation measure. Man-assisted species translocation to environmentally suitable sites may support spontaneous succession after disturbances, as well as the shift of species for which the inherent migration capacity is insufficient to keep up with climate change. This option is primarily advisable in case of aggravating site and stand conditions.

Introduction of species which currently do not occur in Central Europe can be thought of as a questionable approach, mainly because of potential risks to biodiversity and unclear prospects of their long-term vitality. Substantial changes in climate may, however, favour southern species and provenances and they may become alternatives to the current species which may not be able to persist under a drier and warmer climate. For example, the above-mentioned expansion of climates favouring the Mediterranean oak types in Central Europe emphasises the potential importance of the assisted migration.

3.3.2. A selection of pradapted populations and assisted transfer of reproductive material

Concerning the source of reproductive material the rule "local is always best" still finds the consent of both foresters and of environmentalists. Thereby, the idea of assisted migration through the planned transfer of reproductive material is still debated and not yet mainstreamed into forestry practice in the region, while already accepted, for example, in the American Northwest (Marris 2009). Reproductive material from local seed regions provides the reliability of being well-tested if site conditions do not change drastically. If the projected climatic changes are within the range of the expected stability potential of the provenance, adaptation may be achieved through exploiting phenotypic stability. In case of beech, for instance, field tests indicate that the increase of water deficit expressed in terms of an increased Ellenberg climatic quotient of up to 5 units can be buffered through phenotypic stability (plasticity) of the local population (Fig. 2). This buffering effect can, however, be diminished by adverse environmental and ecological factors (Mátyás et al. 2010a; Mátyás & Borovics 2014).

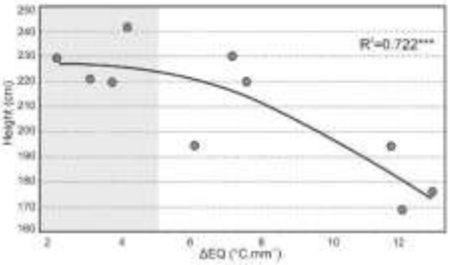

Fig. 2. Decline of 10-year height of 10 beech provenances in response to growing ecological (climatic) distance from the original habitat in the provenance test Bucsuta (Hungary). The transfer is expressed in terms of change of Ellenberg climatic quotient (ΔEQ, °C.mm^{-1}). Positive ΔEQ values indicate that all provenances were transferred into warmer/drier environment. The grey part shows the 5-unit "safety limit" of stability described in the text (Source: Mátyás et al. 2010a, modified).

For planning large-scale transfers of reproductive material from southern sources northward, and from low elevation populations upward, thorough understanding of anticipated changes in local site conditions and knowledge of suitable seed sources is needed. The difficulty of selecting such "preadapted" sources for artificial regeneration lies in the prudent compromise between an optimum match to changing climatic conditions and restraint due to the inherent uncertainty of both climatic projections and unforeseeable biotic risks.

When selecting a source region from which a provenance, which is considered predapted for future conditions at a target location, is to be taken and transferred, both current climate in source region and projected climate in target region need to be evaluated. Such assessment is needed to address the fact that any provenance will respond suboptimally during parts of its lifetime under transient climate change. Mátyás & Borovics (2014) suggested that the current climate in source region should correspond with the climate in the target location during approximately the first third of the expected felling cycle (i.e. for a stand planted in 2015 with a planned felling cycle of 90 years, the projected climate in ca. 2045 should be considered when selecting a source region). However, source regions with desired climates may likely occur outside the range of given species distribution. This fact implies the need for changing tree species composition in target location rather than trying to exploit intra-species adaptation mechanisms in facilitating the forest adaptation.

The selection of alternative provenances is essentially problematic at the xeric limits of the closed forest zone, such as those occurring at the edges of the Slovak and Hungarian plains, which are exposed to excessive summer heat and limited precipitation. There is growing evidence that populations at the xeric limits of a species contain less genetic diversity (Grivet et al. 2011; Borovics & Mátyás 2013) but accumulate alleles of drought tolerance. This, however, means lower adaptive potential (i.e. less phenotypic stability) to changing environmental conditions. These populations are apt to be used primarily as enrichment material or for creating provenance mixtures ("composite provenances", Hubert & Cottrell 2007) to enhance the resilience of regeneration in problematic environments.

3.3.3. Regeneration, tending and thinning

Forest regeneration is especially susceptible to changes in climate (Spittlehouse & Stewart 2003), hence, changes in regeneration methods represent an opportunity to adapt tree species composition to climate change. In natural regenerations, long regeneration phases in small patches should be favoured. For instance, a shift to a fine-grained regeneration mosaic via group selection was found to increase the structural diversity of stands and help to lower the climate change vulnerability of forests in the Eastern Alps (Seidl et al. 2011b). In case of aggravating site conditions, enrichment planting (Lindner et al. 2008), i.e. the combination of natural and artificial regeneration, can be applied. The approach was found to positively influence genetic diversity and thus increase the inherent adaptive capacity of forests. Maintenance of the genetic diversity gains additional importance in climate change adaptation, as genetic diversity was found important in reducing the vulnerability of ecosystems (Seppälä et al. 2009).

Traditional thinning approaches usually lead to structurally and compositionally uniform stands (Nyland 2007), which often result in reduction of forest adaptive capacity (D'Amato et al. 2011). However, adaptation to climate change requires uneven-aged and mosaic forest structures that reduces the impact of disturbances and increase ecological stability. Adaptive silvicultural interventions should minimise the biotic risk after an intervention is performed, support species and structural diversity of stands, support natural regeneration and facilitate water, carbon and nutrients cycling (Seidl et al. 2008a; Seidl et al. 2011b). Close-to-nature-forestry (Krutzsch & Weck 1935) and continuous-cover-forestry (Gadow et al. 2002; Kolström 2011) principles seem to be able to address the forest adaptation to climate change well. Thinning treatments can be applied to reduce the effect of disturbances (Running & Mills 2009). At drought prone sites, thinnings can reduce potential drought stress to trees (Sohn et al. 2013), because they reduce inter-tree competition (Allen et al. 2010), and can improve the recovery of growth after dry periods (Kolström et al. 2011). Intensive thinning was found to reduce the interception losses, and improve the water balance of stands (Slodičák et al. 2011). However, in the short-term, intensive thinnings can increase stand susceptibility to damage (Seppälä et al. 2009; Kolström et al. 2011). Therefore, introduction of risk assessment principles and tools for forest management optimisation seems important to guide the intensity, allocation and timing of silvicultural treatments. Thinning operations, if not systematically done, always contribute to a shift in the genetic variation of the population. Investigations show that medium intensity selective thinning alters genetic composition in an acceptable way, while extreme, vigorous interventions may strongly reduce within-stand genetic variation towards an undesirable, risky state of diminished adaptability (Mátyás & Borovics 2014).

3.3.4. Harvesting

Harvesting operations and harvest timing may substantially modulate forest vulnerability to climate change. In contrast to management under stable environmental conditions, where timber production-related indicators can be primarily used in harvest planning, risk management principles and flexibility of management should be of increased focus in forest management planning under climate change. Large openings should be avoided, as areas devoid of tree canopy may act as heat islands with adverse effects on the forest water cycle. Large clearings can increase the susceptibility of adjacent stands to biotic and abiotic damage (e.g. Lobinger & Skatulla 1996). Also the regeneration in large openings experiences higher exposure to drought and heat, often leading to tree mortality (Haeussler et al. 1995).

Shortening the rotation period can be used to shorten the stand development stage of high susceptibility to insects and diseases (Gottschalk 1995; Seidl et al. 2011b), and has the potential to accelerate the transition to a more suitable species composition (Bolte et al. 2009; Spittlehouse & Stewart 2003). However, a shortening of the rotation period should be considered in combination with all relevant site- and species-specific factors, and needs to balance positive effects on climate risk with effects on wood production, carbon storage, or biodiversity.

For example, an increase in the currently applied rotation period in oak stands in Slovakia was found to be beneficial in the context of timber production (Kulla & Petráš 2012). This potential benefit, however, needs to be balanced with an increasing disturbance risk with stand age. An analysis of species-specific survival probabilities under current climate, management and disturbance regimes (Fig. 3) indicates that

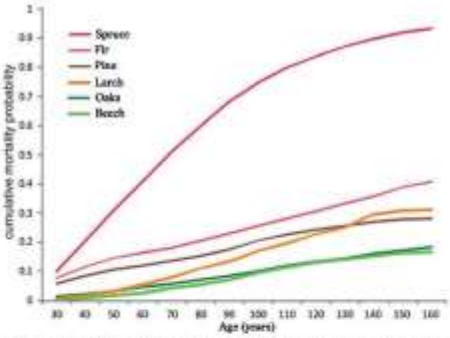

Fig. 3. Cumulative probabilities of main forest tree species to being critically damaged up to a given age. Data are based on sanitation felling records for entire Slovakia for the period 1990–2010, and include the combined effect of all relevant disturbance agents.

disturbance risk increases only moderately for oak and beech (with a survival probability of approximately 90% at age 100), supporting an application of extended rotation periods. The survival probability of Norway spruce, on the other hand, decreases to approximately 25% at age 100 already under current climate in Slovakia, and is likely to decrease further under climate change. This fact highlights the potential of shorter rotation periods for counteracting a climate-mediated increase in disturbance damage, particularly in the conifer-dominated stands in the region. Negative effects of reduced rotation length should also be considered, such as undesired overharvesting and a market surplus of timber supplies, which could potentially have a negative effect on timber economy (Lindner et al. 2008).

3.3.5. Forest protection and disturbance management

The high climatic sensitivity of most forest pests in combination with reduced tree resistance resulting from heat and drought pressure (Desprez-Loustau et al. 2006; Rouault et al. 2006), as well as the anticipated increase in the frequency of droughts and windstorms indicate an increased importance of forest protection and disturbance management under climate change. The currently applied procedures of pest control (e.g. removal of forest residues, wind throw clearings and sanitation felling, use of pesticides) can also be expected to remain effective in the future (Maroschek et al. 2009); intensity, extent, timing and spatial allocation of such measures should, however, be adapted to the changing environmental conditions. The following measures can help to improve current forest protection efforts in responding to climate change: (i) consolidation and harmonization of forest pests monitoring programmes, (ii) broader use of disturbance dynamics and hazard rating models in forest management planning (e.g. Netherer & Nopp-Mayr 2005; Seidl et al. 2014), (iii) broader implementation of principles of integrated pest management and risk management (Waters & Stark 1980; Blennow et al. 2013), and (iv) consolidation of human resources and infrastructure of national forest protection services. A critical aspect for the enhancement of forest protection efficiency is integration of active pest control with silvicultural measures; for example planting pest and drought tolerant species, or reducing the shares of susceptible species and age classes. As seeds and nursery plants are important sources of pathogen dispersal, special care should be paid to aspects of disturbance management in early developmental stages. The fact that some pathogens can remain latent in reproductive material unless drought or other stressors trigger the infection should be considered (Desprez-Loustau et al. 2006).

3.3.6. Other actions

The importance of continuous and long-term forest monitoring increases under climate change as an early identification of development trends in the forest and environment is a prerequisite of adaptive management under changing environmental conditions. Since field monitoring is time and cost-demanding, the importance of remote sensing-based monitoring systems is expected to increase. The long-term evaluation of various biophysical forest indicators using satellite imagery will especially provide critical and near real-time information on the effect of environmental changes and support the adaptive forest management.

Adaptation of forest infrastructure includes the optimisation of forest road networks (Lindner et al. 2008). Increasing the density and improving the quality of forest roads provides accessibility to areas that require sanitation operations, stimulates small-scale management and reduces overharvesting inaccessible locations (Kolström et al. 2011). However, this measure has to be applied with caution as there is strong evidence that improperly built road networks can negatively affect the water regime (Smerdon et al. 2009), and thus amplify the adverse effects of drought.

The forest planning infrastructure also needs to be improved, as many current planning tools such as yield tables and empirical models are not able to address the effects of a changing environment. In this regard it is increasingly important to consider climate sensitive processes explicitly in models used for planning (e.g., Seidl et al. 2011c), and to improve the linkages between process-based modelling and the decision support systems used in practical forest management (Wolfslehner & Seidl 2010).

Although most of the measures mentioned above addressed a forest stand scale and primarily concerned forest management, there is a range of cross-sectoral measures which focus on watershed or landscape scales. Adaptation measures at a landscape scale should mainly support the connectivity of ecosystems, create and/or maintain corridors between separated forested areas, and avoid forest fragmentation (Lindner et al. 2008; Running & Mills 2009; Seppälä et al. 2009). These measures should support the natural migration of species and gene flow, and thus enhance the effect of inherent adaptation mechanisms of forests. Forest adaptation can also aim at the enhancement of diverse forest regulation functions, which can be used to moderate the adverse effects of climate on landscape, including water regulation and flood prevention (Buttle 2011; Hlásny et al. 2013).

4. Conclusions

Forest responses to climate change are highly complex, and our understanding of potential impacts and sensitivities is still limited. Despite such limitations, it is possible and necessary to develop and implement climate change adaptation strategies already now (Spittlehouse & Stewart 2003). All forest management decisions are taken in face of uncertainty about the future, and delaying the implementation of adaptation measures in expectation of improved knowledge will likely lead to perpetual inaction. However, a thorough uncertainty assessment with regard to the expected climate change impacts can help to assess the need and likely success of adaptation measures. Both climatic uncertainty and societal uncertainty, for example that related to changing demands on ecosystems, need to be addressed (Seidl & Lexer 2013). Furthermore, an explicit consideration of the possible effects of adaptive management on a variety of locally important ecosystem services and an assessment of possible trade-offs with regard to their societal acceptance are needed.

Currently, climate change adaptation is often not addressed in forest management deliberately, but rather manifests itself in response to impending threats, such as pest epidemics or windthrows. In facing such threats, finer-grained and close-to-nature forest management systems are increasingly applied, while large-scale even-aged systems have been restricted to a narrow set of conditions in most of Central Europe. Accordingly, silvicultural approaches that promote a natural species composition, close-to-nature forest structure, and natural regeneration have gained traction in recent decades in all Central European countries. Such practices represent key starting points and opportunities for climate change adaptation. Yet, the profound changes expected for the future might require more systematic and targeted adaptation efforts going beyond what is currently implemented.

This paper stressed key processes and actions which need to be addressed to facilitate effective forest adaptation. First, an understanding of inherent adaptation mechanisms acting at species and genetic levels, and a thorough consideration of such mechanisms in forest management are critical prerequisites for effective adaptation. Second, the role of risk assessment in forest management planning for changing environmental conditions is becoming increasingly important. Thereby, the historically strong focus of planning on timber production will need to be broadened in many areas, not only to accommodate the concept of multifunctional forestry but also to ensure acceptable levels of risk in ecosystem services provisioning. Third, the information on long-term forest responses to climatic and other stressors needs to be improved. However, the technical and organisational frameworks of the current forest monitoring systems in the region as well as the ensuing utilisation of the collected data are not yet geared towards supporting adaptive forest management. Hence, a consolidation of monitoring systems and a strengthening of information transfer to management decision makers are required. Fourth, despite an increasing availability of climate projections and regional vulnerability studies, the application of such information in forest management decision making is still limited. To promote the use of this information, actions on increasing of the awareness of managers and stakeholders need to be taken, and legislative support to adaptation processes need to be improved. Although forest adaptation is already included in many national forestry strategies, programmes and actions, these documents do not per se ensure an efficient and systematic implementation of such measures in forestry practice. Ultimately, successful adaptation decisions depend on skilled professionals, which is highlighting the importance of improved forest education. To conclude, we advocate a mainstreaming of climate change issues into all realms of forestry – from education to policy and from monitoring to management planning – in order to make the forests of Central Europe fit for a changing future.

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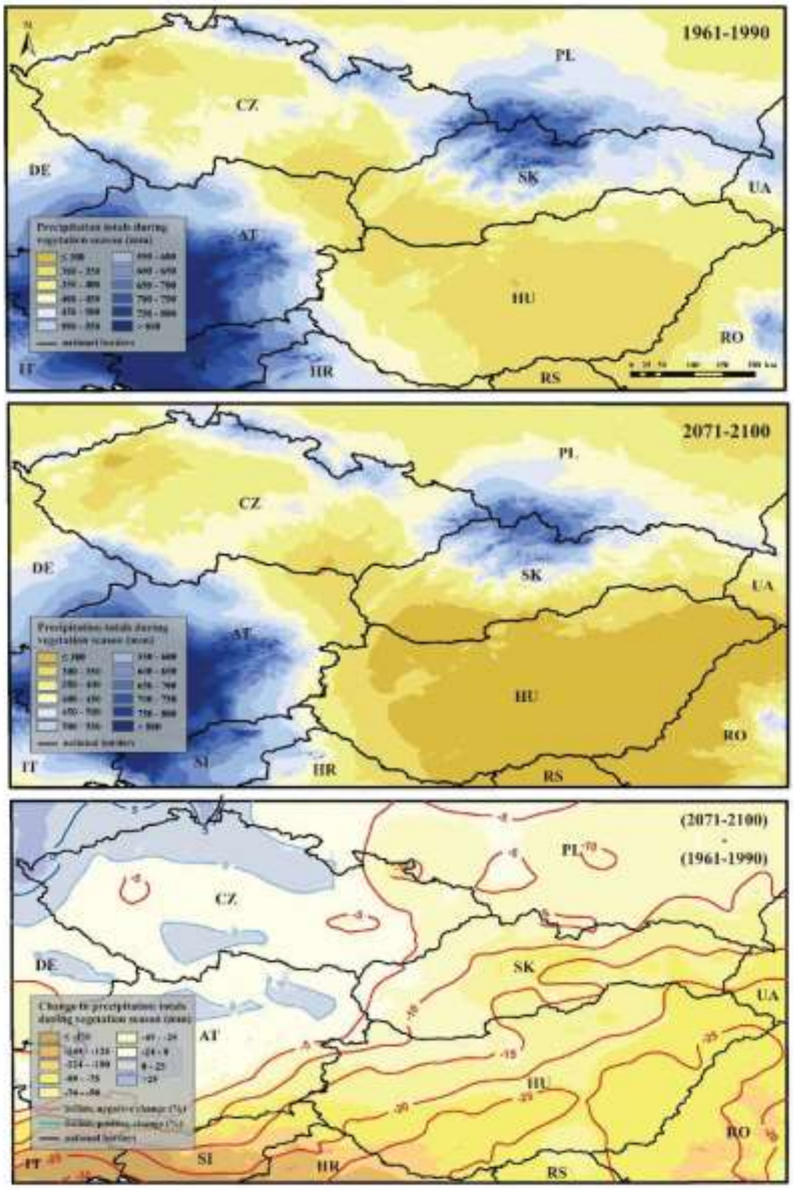
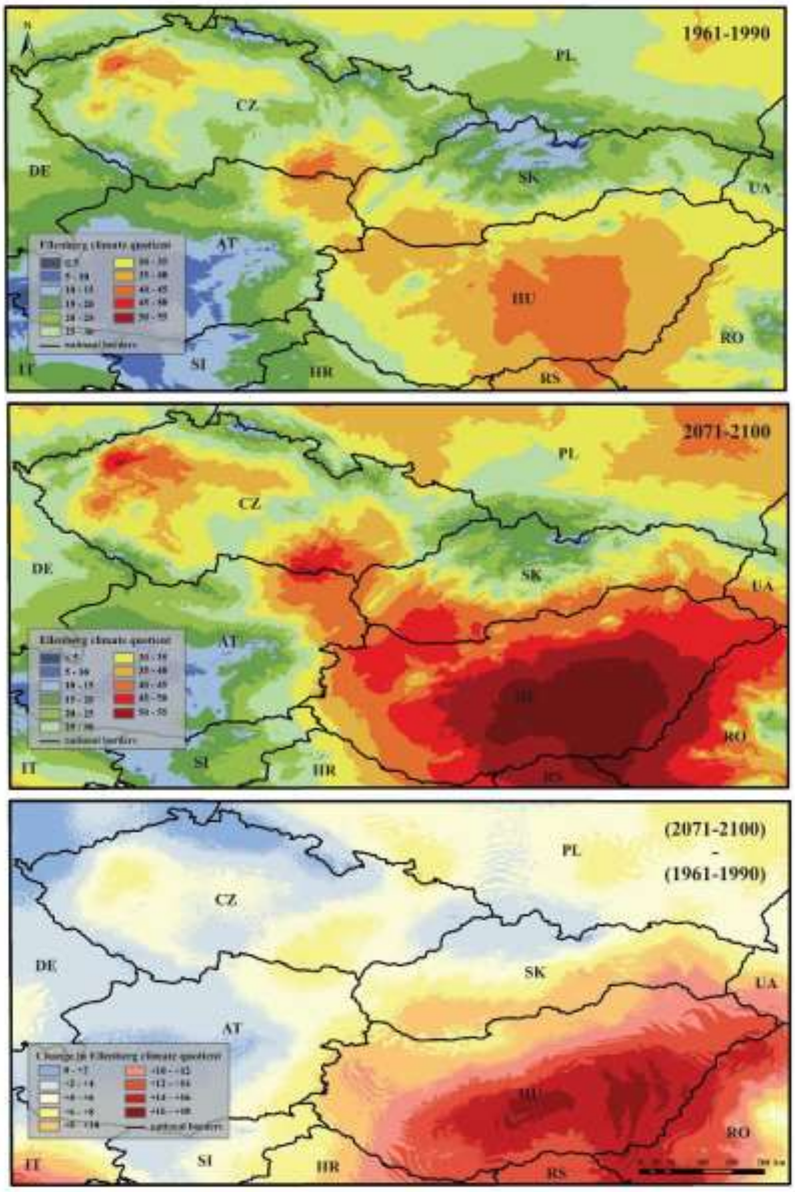
Annex 1: Precipitation distribution (April–September) in Central Europe in the period 1961–1990 based on observed meteorological data, and calculated as an average of 10 regional climate models for the period 2071–2100. A difference and percentage change map is given as well.



Annex 2: Distribution of the Ellenberg climatic quotient in Central Europe in the period 1961–1990 based on observed meteorological data, and calculated as an average of 10 regional climate models for the period 2071–2100. A difference map is given as well.



6. Diskuze, závěr a doporučení pro praxi

Tato práce představuje soubor publikovaných vědeckých studií, ze kterých každá zahrnuje relativně obsáhlou diskusi. Z tohoto důvodu zde nebudeme opakovat diskuse k jednotlivým studiím, podobně jako při formulaci výsledků v kapitole 5. Diskutovány budou klíčové průřezové oblastí obecně se týkající řešené problematiky.

6.1 Zdrojová data

Všechny části řešení zaměřující se na celý region Karpat čelily problému ohledně dostupnosti dat o lese, stanovištních podmínkách, ochraně přírody nebo rozšíření škůdců. Obecnou zkušeností je, že realizace nadnárodních studií je mimořádně ztížená problematickou dostupností a nízkou kvalitou většiny dat (Badea et al. 2004, Percy a Ferreti 2004, Tröltzsch et al. 2009). Některá data jsou ve vysoké kvalitě dostupná na národních úrovních (lesní hospodářské plány, inventarizace lesa apod.), jejich sdílení pro účely mezinárodního výzkumu je však z legislativních důvodů v podstatě nemožné. Pro tyto účely byly evropskými organizacemi jako Evropská environmentální agentura nebo Spojené výzkumné centrum vypracovány datové vrstvy s celoevropskou nebo globální pokryvností (např. Bartholomé a Belward 2005, Ahlenius 2012). Bohužel na základě výsledku publikace Trombik a Hlásny 2013 (Kapitola 5.1) je kvalita těchto dat (např. o dřevinné skladbě lesa) nízká a může zpochybňovat výsledky některých studií. Pozitivním příkladem v oblasti pro vědeckou veřejnost volně dostupných dat jsou stále se zlepšující klimatická data z různých databází, jako je např. v této práci použitá FORESEE (Dobor et al. 2015) nebo CarpatClim (Spinoni et al. 2015). Jako kritický problém při nadnárodních výzkumech lze v současnosti vnímat problematickou dostupnost dat o lesních škůdcích a obecně disturbancích a v podstatě neexistující sdílení dat národních lesnických služeb a podobných agentur. S ohledem na vysokou dynamiku škůdců v podmínkách změny klimatu jsou poznatky o jejich výskytu, přemnožení, nebo změnách v populační dynamice v širším regionu střední Evropy klíčové z hlediska adaptace a schopnosti adekvátně reagovat (Seidl et al. 2011, 2014). Data použitá ve studiích prezentovaných v této práci (včetně certifikovaných map v příloze) byla získána převážně na bázi osobních kontaktů, což rozhodně nepředstavuje optimální východisko pro výzkum a tato skutečnost také omezuje možnosti ochrany lesa realizovat účinná opatření. Obecným problémem je různá struktura národních dat, která omezuje až znemožňuje jejich integraci s jinými daty (např. sběr dat pro různé taxonomické úrovně škůdců). Neméně potěšující skutečností je, že nejsou patrné téměř žádné snahy pro zlepšení tohoto stavu.

6.2 Scénáře změny klimatu

V této práci byla použita starší generace scénářů změny klimatu řízená scénářem emisí skleníkových plynů A1B. Důvodem bylo, že příprava řešení této práce probíhala v období, kdy projekce založené na tzv. Representative Concentration Pathways nebyly pro zájmové území běžně dostupné ve formě přímo využitelné pro dopadové studie (např. po korekci biasu). Použití pouze jednoho emisního scénáře také napovídá, že celková neurčitost výsledků simulací může být podhodnocena (Spinoni et al. 2015). Naopak výhodou je poměrně snadná porovnatelnost s množstvím předešlých prací, ve kterých byly scénáře řízené emisním scénářem A1B hojně využívány (Belda et al. 2015, Spinoni et al. 2015). V dalších studiích již počítáme s využíváním podskupiny projekcí změny klimatu řízených RCP4.5 a RCP8.5, které v dostatečné míře zachycují variabilitu budoucího vývoje klimatu a jsou standardně využívány v různých dopadových studiích (Ward et al. 2012).

6.3 Případové studie

Studie prezentované formou publikovaných vědeckých prací zahrnují různé aspekty vlivu změny klimatu na ekosystémy Karpat, dynamiku škůdců a simulovaný vývoj lesa v podmínkách působení disturbancí a změny klimatu. Ačkoli se tento soubor prací může jevit nesourodý, poskytuje vhodná východiska pro formulaci opatření a doporučení pro management lesa publikovaných formou studií Hlásny et al. 2014 a 2017a,b. V žádné studii však nebyl přímo řešen jeden z nejkomplexnějších problémů ekologie lesa, kterým je vliv změny klimatu na disturbanční režimy lesa (Dale et al. 2001, Lindner et al. 2010, Turner 2010). Tento přístup je doménou procesních modelů, které umožňují hodnotit interakce měnícího se klimatu s fyziologickým stavem stromů (mírou stresu) nebo parametry populační dynamiky škůdců (reprodukce, voltinizmus, mortalita v zimním období apod.) (např. Seidl et al. 2011, 2014). Komplexními interakcemi těchto částkových procesů je definován charakter (budoucího nebo obecně alternativního) disturbančního režimu (Turner 2010). Vědecké studie prezentované v této dizertační práci se opíraly o empirické nebo statistické modelování, které obecně předpokládá platnost minulých ekologických vztahů i v podmínkách změněného (neanalogického) klimatu. Je zřejmé, že tento předpoklad má pouze omezenou platnost (Seidl et al. 2011, 2014). Příkladem je např. vyvinutý statistický model pro prognózování gradací bekyně velkohlavé nebo využití modelu Sibyla pro hodnocení produkce a mortality lesních porostů. Prognostický model gradací mnišky přepokládal, že fluktuace charakteristické pro poslední desetiletí budou platit i v budoucnosti. Tento model však nezahrnuje možný kolaps gradací v důsledku např. změněného režimu přirozených nepřátel nebo obecně nejasné klimatické vlivy na velikost areálů přemnožení a jejich načasování (Parmesan et al. 1999, Vanhanen et al. 2007). Tyto parametry jsou kromě reakce škůdce na změněné podmínky závislé i na budoucím stavu a dostupnosti hostitelských dřevin (Franklin et al. 2002, Lindner et al. 2010), která nebyla zohledněna. Jak již bylo uvedeno, řešením je využití komplexních procesních ekosystémových modelů, které jsou však v současnosti dostupné pouze pro některé škůdce resp. typy disturbancí (Gardiner a Quine 2000).

V případě simulací poškozování lesa pomocí modelu Sibyla byly statistické parametry disturbancí odvozeny z dobových dat získaných z lesní hospodářské evidence. Zatímco růstový proces v modelu Sibyla byl ovlivněn změnou klimatu, parametry disturbancí (v textů zmíněné pravděpodobnosti přežívaní) byly stabilní po celou dobu vývoje porostu, resp. měnily se jen v závislosti na změně dřevinné a věkové skladby. Faktory jako je např. zvýšený tlak podkorního hmyzu v důsledku nárůstu počtu generací nebo fyziologického oslabení dřevin nijak zohledněny nebyly. Obdobně jako v předešlém případě je i tato problematika v zájmu autorova i obecně ekologického budoucího výzkumu.

6.4 Navržená opatření pro management lesa

Adaptace na změnu klimatu a související adaptace na zvýšenou frekvenci a intenzitu lesních disturbancí, možnou invazi nových škůdců, nebo na celkovou změnu disturbančního režimu s rostoucím významem sucha a požárů, se týká všech oblastí managementu lesa, včetně ochrany (Baur et al. 2003, Prestemon a Holmes 2004). Prezentované výsledky poukázaly na rizika související např. s invazí nových druhů (lýkožrout severský) nebo s neudržitelností hospodaření orientovaného na smrkové monokultury. Analýzou současného stavu v regionu bylo poukázáno na neexistenci nadnárodních systémů zaměřených např. na monitoring invazních škůdců resp. obecně na účinné sdílení lesnických dat, které může zlepšit připravenost lesnictví v regionu

Karpat a obecně střední Evropy na dopady změny klimatu a s tím související zvýšenou intenzitu disturbancí.

Pochopit a kvantifikovat možné dopady klimatických změn na lesní ekosystémy představuje mimořádně komplexní a interdispciplinární problematiku a naše současné poznatky a obecné chápání citlivosti, exponovanosti a adaptační kapacity lesa je stále poměrně omezené. I přes tyto limity je definice a implementace adaptačních strategií klíčovým a nezbytným úkolem lesního hospodářství (Spittlehouse a Stewart 2003). V současné době se adaptace na změnu klimatu v lesním hospodářství často omezuje pouze na reakce na blížící se hrozby, jako jsou přemnožení škůdců nebo větrné vichřice. Proto v posledních desetiletích získaly lesnické postupy, které podporují přírodě blízké dřevinné složení lesů, diverzifikaci struktury lesa nebo přirozenou obnovu, značnou pozornost ve všech středoevropských zemích. V oblasti ochrany lesa při reakci na změnu klimatu lze za klíčové strategické opatření považovat: (i) konsolidaci a harmonizaci programů monitorování lesních škůdců, (ii) širší využívání modelů citlivosti a dynamiky lesních škůdců při lesohospodářském plánování (např. Netherer a Nopp-Mayr 2005, Seidl et al. 2014), (iii) širší implementaci principů integrované ochrany (Blennow et al. 2013). Kritickým aspektem pro zvýšení účinnosti ochrany lesů je integrace aktivní ochrany proti škůdcům, například využití dřevin odolných vůči suchu. Tyto praktiky představují klíčové výchozí body a příležitosti pro přizpůsobení se změně klimatu. Komplexní a intenzivnější změny, které se očekávají v budoucnosti, však mohou vyžadovat systematičtější a cílenější adaptační úsilí, které překračuje rámec současných poznatků a využívaných postupů.

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Přílohy

Příloha č.1 Soubor map: Dopad klimatických změn na populace lýkožrouta severského (*Ips duplicatus*, Coleoptera: Curculionidae) v Karpatech: Vliv na distribuci a populační dynamiku.

SOUBOR MAP: DOPAD KLIMATICKÝCH ZMĚN NA POPULACE LÝKOŽROUTA SEVERSKÉHO (IPS DUPLICATUS, COLEOPTERA: CURCULIONIDAE) V KARPATECH: VLIV NA DISTRIBUCI A POPULAČNÍ DYNAMIKU

Tomáš Hlásny, Jiří Trombik, Jaroslav Holuša & Karolina Lukášová

Přirozený areál výskytu lýkožrouta severského (*Ips duplicatus*) zahrnuje Palearktické oblasti od Skandinávie, severo-východní a střední Evropu a severo-východní Asii (Pfeffer a Knížek 1995). Až do 20. století byl nejjižnější výskyt *I. duplicatus* v Evropě v Bělověžském pralese (Puszcza Bialowieska, severní Polsko). Od první poloviny 20. století se *I. duplicatus* začal šířit na jih do nepůvodních smrkových porostů v nížinách i vrchovinách (Pfeffer a Knížek 1995). Rychlost, kterou se distribuční areál lýkožrouta severského rozšiřuje v Evropě ukazuje, že tento druh pozitivně reaguje na globální změnu klimatu (Holuša et al. 2010). *I. duplicatus* pozitivně reaguje na vyšší teploty, kde má zpravidla multivoltinní životní cyklus. V současnosti se líhne jedna generace ročně v tajze a severním Polsku, ve střední Evropě generace 2-3.

V posledních letech byl výskyt *I. duplicatus* dokumentován v jižním Polsku, České republice, Slovensku, Rakousku a Německu. Přestože je *I. duplicatus* adaptován na chladné severské podmínky, zpravidla se ve střední Evropě nevyskytuje uvnitř rozsáhlých hor. Lokální gradace byly v Karpatech dokumentovány v Polsku a České republice (Knížek a Zahradník 1996, Grodzki 2003), ale pouze do nadmořských výšek cca 600 m n.m. V Rumunsku byl výskyt *I. duplicatus* zaznamenán až do výšky cca 1 000 m n.m. V současnosti je lýkožrout severský považován za ekonomicky významného škůdce, jehož význam stále roste.

Analýza vývoje lýkožrouta severského byla založena na modelu PHENIPS – Komplexním fenologickém modelu původně navrženém pro lýkožrouta smrkového *Ips typographus* (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vzduchu den nástupu napadení a průměrná teplota kůry rychlost vývoje jednotlivých vývojových stadií, teplotní limity pro jednotlivá stadia byly určeny na základě práce Wermelinger a Seifert (1998).

Přestože se v porovnání s lýkožroutem smrkovým jedná o menší druh (Pfeffer 1955), a mohl by tedy potřebovat menší kumulativní teploty potřebné pro svůj vývoj, v podmínkách střední Evropy *I. duplicatus* zpravidla kopíruje fenologický model *I. typographus* (Holuša et al. 2012). Hlavním rozdílem je fakt, že se *I. duplicatus* nevyskytuje ve vysokých nadmořských výškách (Holuša et al. 2010), ale preferuje polohy do 800 m n.m. (Holuša et al. 2013).

Pro definování výškového limitu byla použita data z odchytů ve feromonových lapačích. V západních Karpatech byly lapače umístěny v pravidelných 100 metrových intervalech na hoře Ostrý (Moravskoslezské Beskydy) v letech 2002 a 2003 (Holuša 2004), pro východní Karpaty byly použity výsledky studie Duduman et al. 2011. Na základě výsledků měření byl výškový limit výskytu *I. duplicatus* stanoven na 800 m n.m. pro západní a 1 000 m n.m. pro východní Karpaty.

Klimatická data za období 1951-2007 byla převzata z databáze E-OBS (Haylok et al. 2008). Data o budoucím klimatu (2007-2100) byla převzata z výsledků projektu ENSEMBLES (van der Linden a Mitchell 2009). Pro potřeby vytvoření klimatických map Karpat byla použita interpolační technika krigování s externím driftem (Hudson a Wackernagel 1994, Goovaerts 2000), přičemž byla použita nadmořská výška jako podpůrná proměnná, korelována s většinou klimatických prvků. Data o rozšíření smrku ztepilého v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, prediktivního mapování a národních lesnických statistik (Brus et al. 2011). Výsledkem jsou rastrové mapy s rozlišením 1x1 km, nesoucí informace o zastoupení dané dřeviny. Pro účely této práce byly mapy korigovány na základě dat Corine Landcover. Výsledné mapy byly vytvořeny pro tři časová období – referenční klima (1961-1990), klima v blízké budoucnosti (2021-2050) a klima ve vzdálené budoucnosti (2071-2100).

POUŽITÁ LITERTURA

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Lýkožrout severský (***Ips duplicatus***) v Karpatech: Předpokládaný počet generací za rok v období 1961-1990

Tomáš Hlásny, Jiří Trombik, Jaroslav Holuša & Karolina Lukášová

LÝKOŽROUT SEVERSKÝ

Přirozený areál výskytu lýkožrouta severského (*Ips duplicatus*) zahrnuje Palearktické oblasti od Skandinávie, severo-východní a střední Evropy a severo-východní Asii (Pfeffer a Knížek 1995). Od první poloviny 20. století se *I. duplicatus* začal šířit na jih do nepůvodních smrkových porostů v nížinách i vrchovinách (Pfeffer a Knížek 1995). Rychlost, kterou se distribuční areál lýkožrouta severského rozšiřuje v Evropě, ukazuje, že tento druh pozitivně reaguje na globální změnu klimatu (Holuša et al. 2010). *I. duplicatus* pozitivně reaguje na vyšší teploty, kde má zpravidla multivoltinní životní cyklus.
V současnosti se líhne jedna generace ročně v tajze a severním Polsku, ve střední Evropě generace 2-3.

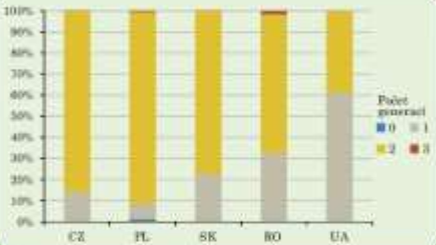
V posledních letech byl výskyt *I. duplicatus* dokumentován v jižním Polsku, České republice, Slovensku, Rakousku a Německu. Přestože je *I. duplicatus* adaptován na chladné severské podmínky, zpravidla se ve střední Evropě nevyskytuje uvnitř rozsáhlých hor. Lokální gradace byly v Karpatech dokumentovány v Polsku a České republice (Knížek a Zahradník 1996, Grodzki 2003), ale pouze do nadmořských výšek cca 800 m n.m. V Rumunsku byl výskyt *I. duplicatus* zaznamenán až do výšky cca 1 000 m n.m. V současnosti je lýkožrout severský považován za ekonomicky významného škůdce, jehož význam stále roste.

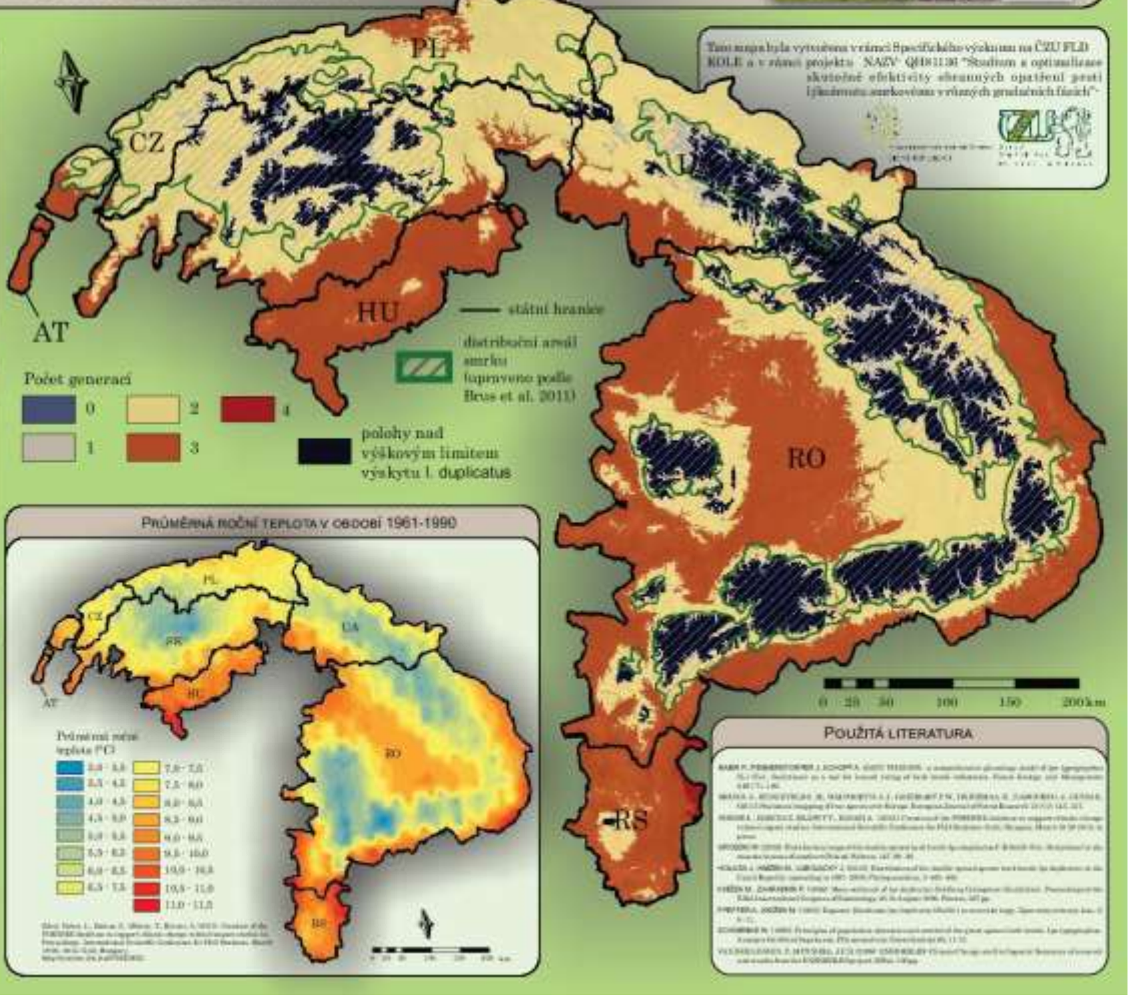
POUŽITÁ DATA A METODY

Analýza vývoje lýkožrouta severského byla založena na modelu PHENIPS – Komplexním fenologickém modelu lýkožrouta smrkového *Ips typographus* (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vzduchu den nástupu napadení a průměrná teplota kůry rychlost vývoje jednotlivých vývojových stadií. Výsledky modelování byly dále upraveny pomocí digitálního výškového modelu, na jehož základě byl definován horní výškový limit výskytu *I. duplicatus* (800 m n.m. pro západní a 1 000 m n.m. pro východní Karpaty).

Klimatická data byla převzata z databáze FORESEE (Dobor et al. 2012), která obsahuje modifikované výsledky regionálních klimatických simulací provedených v rámci projektu ENSEMBLES (Van der Linden et al. 2009). Data o rozšíření smrku ztepilého v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, prediktivního mapování a národních lesnických statistik (Brus a kol. 2011). Pro účely této práce byly mapy korigovány na základě dat Corine Landcover.

PROCENTUÁLNÍ ZASTOUPENÍ SMRKOVÝCH POROSTŮ UVNITŘ DISTRIBUČNÍHO AREÁLU LÝKOŽROUTA SEVERSKÉHO V KARPATSKÝCH ZEMÍCH UMOŽŇUJÍCÍ VÝVOJ URČITÉHO POČTU GENERACÍ V OBDOBÍ 1961-1990





PRŮMĚRNÁ ROČNÍ TEPLOTA V OBDOBÍ 1961-1990

Zdroj: [illegible]

Tato mapa byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH81136 "Studium a optimalizace skutečné efektivity obranných opatření proti lýkožroutu smrkovému v různých gradačních fázích".

POUŽITÁ LITERATURA

[illegible]

Lýkožrout severský (***Ips duplicatus***) v Karpatech: Předpokládaný počet generací za rok v období 2021-2050

Tomáš Hlásny, Jiří Trombik, Jaroslav Holuša & Karolina Lukášová

POUŽITÁ DATA A METODY

Analýza vývoje lýkožrouta severského byla založena na modelu PHENIPS – Komplexním fenologickém modelu lýkožrouta smrkového *Ips typographus* (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vzduchu den nástupu napadení a průměrná teplota kůry rychlost vývoje jednotlivých vývojových stadií. Výsledky modelování byly dále upraveny pomocí digitálního výškového modelu, na jehož základě byl definován horní výškový limit výskytu *I. duplicatus* (900 m n.m. pro západní a 1 000 m n.m. pro východní Karpaty).

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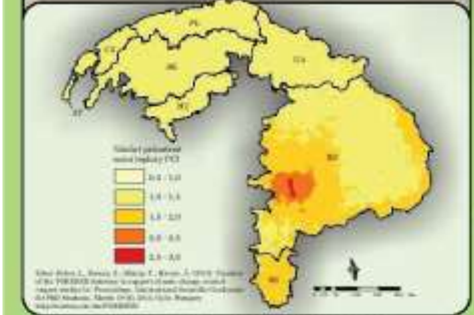
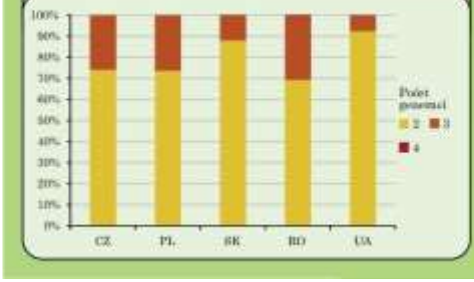
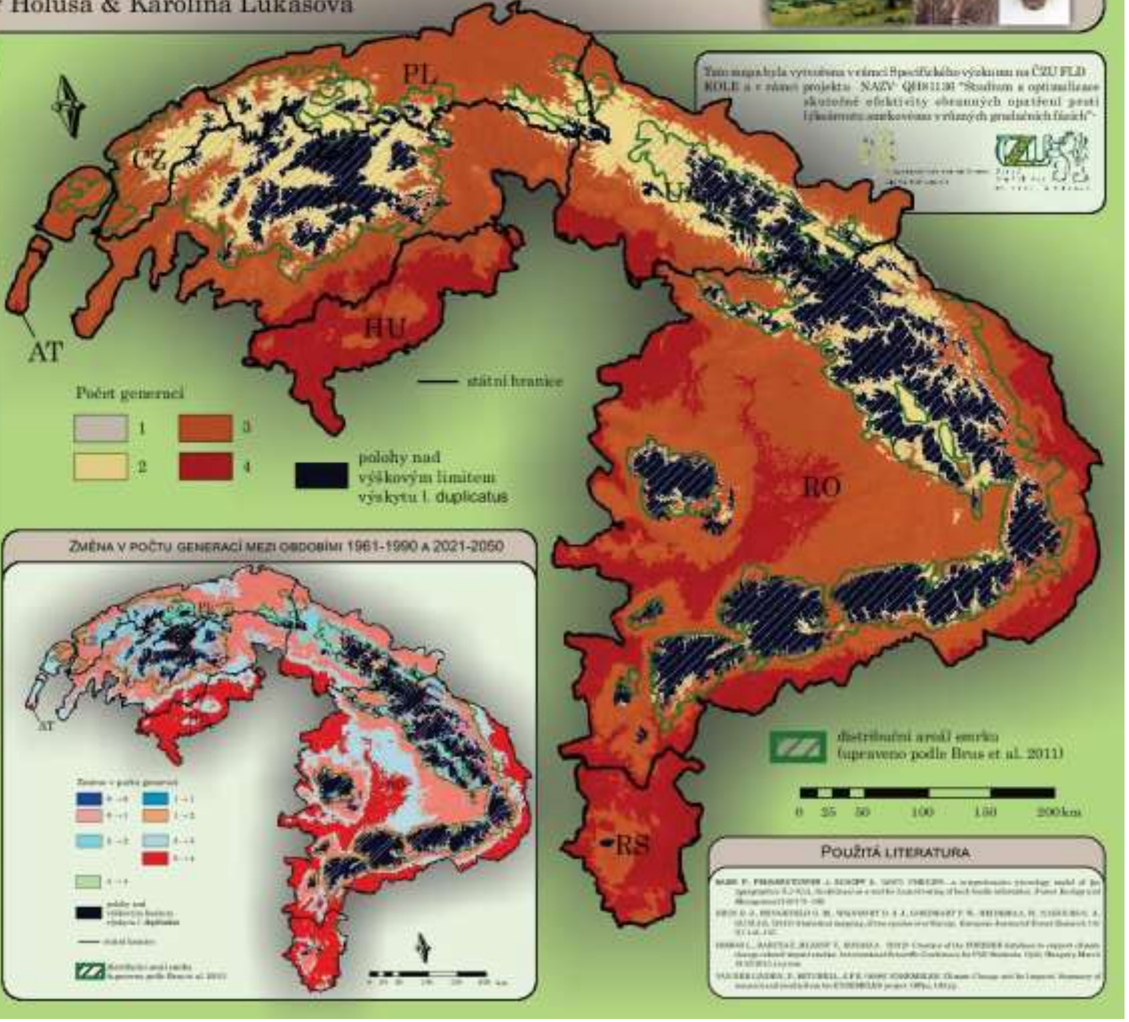
ZMĚNA PRŮMĚRNÉ ROČNÍ TEPLOTY MEZI OBDOBÍMI 1961-1990 A 2021-2050



PROCENTUÁLNÍ ZASTOUPENÍ SMRKOVÝCH POROSTŮ V KARPATSKÝCH ZEMÍCH UMOŽŇUJÍCÍ VÝVOJ URČITÉHO POČTU GENERACÍ LÝKOŽROUTA SEVERSKÉHO V OBDOBÍ 2021-2050

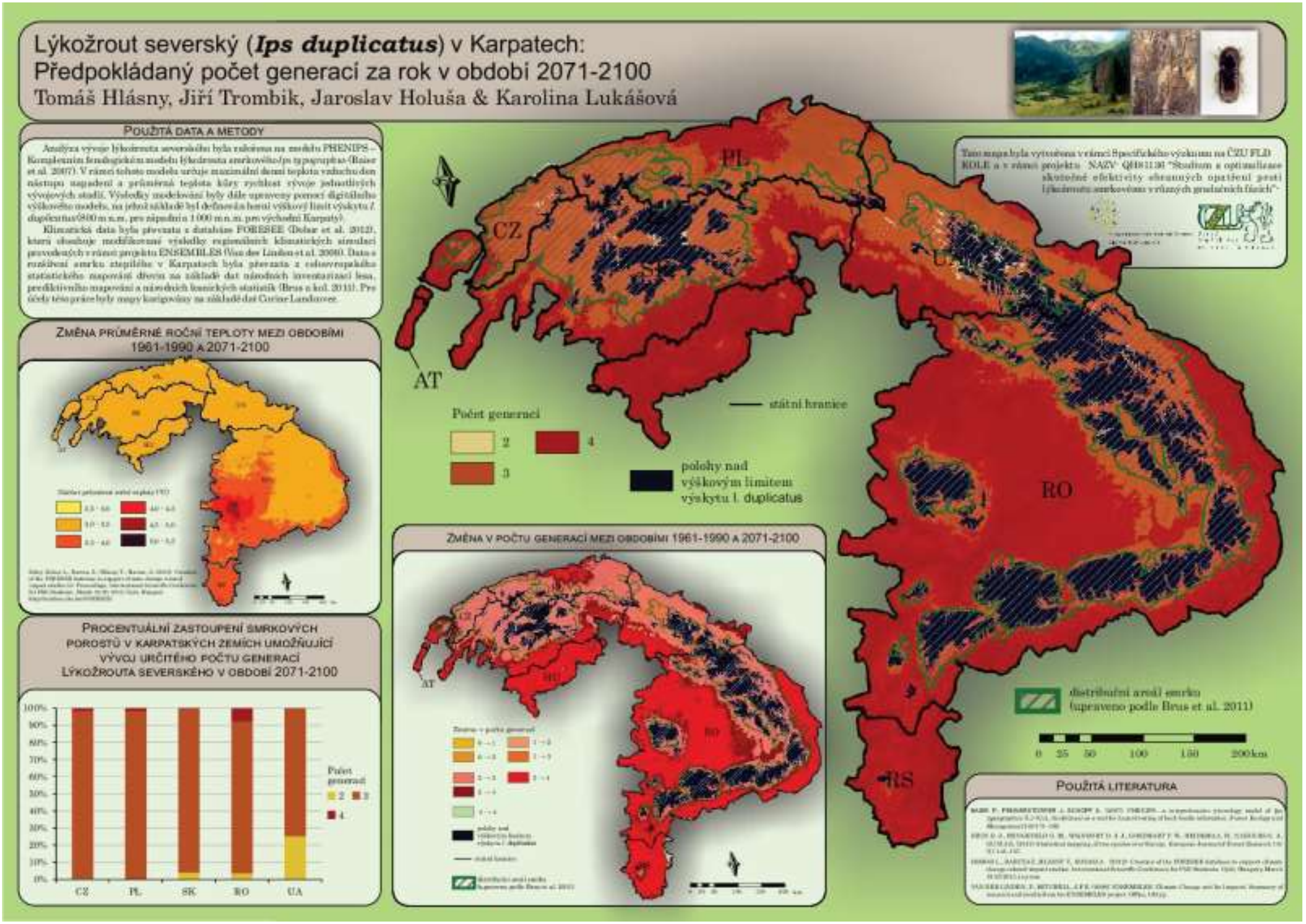


Tato mapa byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH81136 "Studium a optimalizace skutečné efektivity obranných opatření proti lýkožroutu smrkovému v různých gradačních fázích".



ZMĚNA V POČTU GENERACÍ MEZI OBDOBÍMI 1961-1990 A 2021-2050

POUŽITÁ LITERATURA



Lýkožrout severský (***Ips duplicatus***) v Karpatech: Předpokládaný počet generací za rok v období 2071-2100

Tomáš Hlásny, Jiří Trombik, Jaroslav Holuša & Karolina Lukášová

POUŽITÁ DATA A METODY

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ZMĚNA PRŮMĚRNÉ ROČNÍ TEPLOTY MEZI OBDOBÍMI 1961-1990 A 2071-2100

ZMĚNA V POČTU GENERACÍ MEZI OBDOBÍMI 1961-1990 A 2071-2100

PROCENTUÁLNÍ ZASTOUPENÍ SMRKOVÝCH POROSTŮ V KARPATSKÝCH ZEMÍCH UMOŽŇUJÍCÍ VÝVOJ URČITÉHO POČTU GENERACÍ LÝKOŽROUTA SEVERSKÉHO V OBDOBÍ 2071-2100

POUŽITÁ LITERATURA

Příloha č.2 Soubor map: Dopad klimatických změn na populace lýkožrouta smrkového (*Ips typographus*, Coleoptera: Curculionidae) v Karpatech: Vliv na distribuci a populační dynamiku.

SOUBOR MAP: DOPAD KLIMATICKÝCH ZMĚN NA POPULACE LÝKOŽROUTA SMRKOVÉHO (IPS TYPOGRAPHUS, COLEOPTERA: CURCULIONIDAE) V KARPATECH: VLIV NA DISTRIBUCI A POPULAČNÍ DYNAMIKU

Tomáš Hlásny, Jiří Trombik, Jaroslav Holuša & Karolina Lukášová

Lýkožrout smrkový (*Ips typographus*, Coleoptera: Curculionidae) patří mezi nejvýznamnější škůdce smrkových porostů v Evropě. Napadá především čerstvě vytěžené smrkové dříví, padlé smrky v polomech (Forster 1993) anebo z nejrůznějších příčin fyziologicky oslabené stojící stromy (Schwenke 1996). Jakmile nemá dostatek vhodných stromů pro zakládání potomstva, začne napadat i zdravé stojící smrky. Škodlivost lýkožrouta je úzce svázaná se zdravotním stavem porostů a vhodnými klimatickými podmínkami na daném místě.

V současnosti se zpravidla líhnou dvě generace lýkožrouta smrkového za rok, ve vyšších polohách jedna a při teplém průběhu počasí může být o jednu generaci více. Vyvíjí se téměř výhradně na smrku ztepilém (*Picea abies*), výjimečně na modřínu opadavém (*Larix decidua*).

U lýkožrouta smrkového se předpokládá zkrácení doby vývoje, což mu umožní ukončit životní cyklus dříve a založit další generace během sezóny (Lange et al. 2006). Změna klimatu také ovlivní rojení, diapauzu a zimní mortalitu tohoto škůdce. Teplotní režim v průběhu podzimu by pak měl rozhodující vliv na velikost populace během rojení na jaře následujícího roku (Jönsson et al. 2009).

Analýza vývoje lýkožrouta smrkového byla založena na modelu PHENIPS – Komplexním fenologickém modelu lýkožrouta smrkového *Ips typographus* (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vzduchu den nástupu napadení a průměrná teplota kůry určuje rychlost vývoje jednotlivých vývojových stadií, teplotní limity pro jednotlivá stadia byly určeny na základě práce Wermelinger a Seifert (1998).

Klimatická data za období 1951-2007 byla převzata z databáze E-OBS (Haylok et al. 2008). Data o budoucím klimatu (2007-2100) byla převzata z výsledků projektu ENSEMBLES (van der Linden a Mitchell 2009). Pro potřeby vytvoření klimatických map Karpat byla použita interpolační technika krigování s externím driftem (Hudson a Wackernagel 1994, Goovaerts 2000), přičemž byla použita nadmořská výška jako podpůrná proměnná, korelována s většinou klimatických prvků. Data o rozšíření smrku ztepilého v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, prediktivního mapování a národních lesnických statistik (Brus et al. 2011). Výsledkem jsou rastrové mapy s rozlišením 1x1 km, nesoucí informace o zastoupení dané dřeviny. Pro účely této práce byly mapy korigovány na základě dat Corine Landcover. Výsledné mapy byly vytvořeny pro tři časová období – referenční klima (1961-1990), klima v blízké budoucnosti (2021-2050) a klima ve vzdálené budoucnosti (2071-2100).

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Tato práce byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH91097 „Vyhodnocení dopadu globálních klimatických změn na rozšíření a voltinizmus *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) ve smrkových porostech České republiky jako východisko pro jejich trvale udržitelný management."

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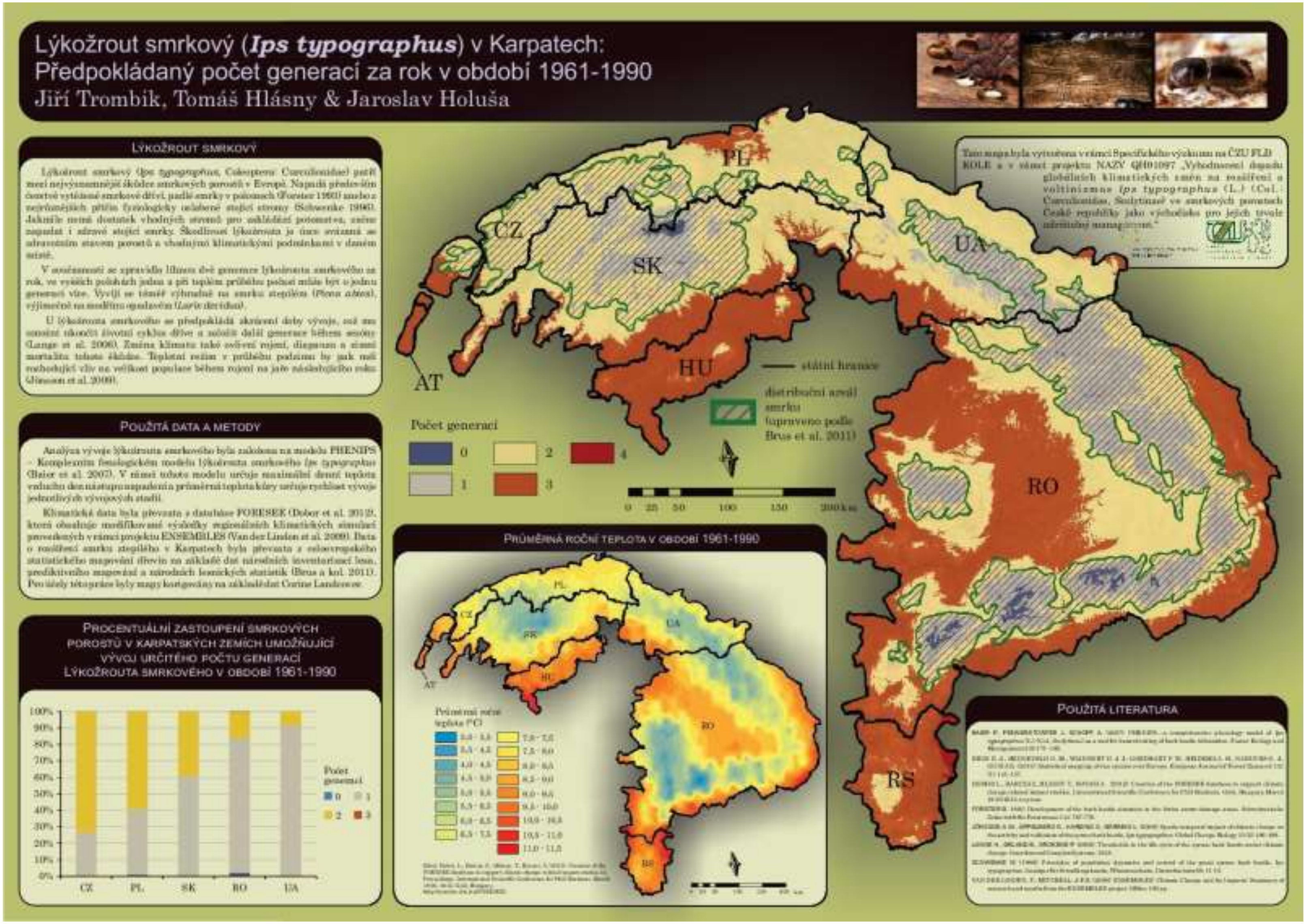

Lýkožrout smrkový (***Ips typographus***) v Karpatech: Předpokládaný počet generací za rok v období 1961-1990

Jiří Trombik, Tomáš Hlásny & Jaroslav Holuša

LÝKOŽROUT SMRKOVÝ

Lýkožrout smrkový (*Ips typographus*, Coleoptera: Curculionidae) patří mezi nejvýznamnější škůdce smrkových porostů v Evropě. Napadá především čerstvě vytěžené smrkové dříví, padlé smrky v polomech (Forster 1993) anebo z nejrůznějších příčin fyziologicky oslabené stojící stromy (Schwenke 1996). Jakmile nemá dostatek vhodných stromů pro zakládání potomstva, začne napadat i zdravé stojící smrky. Škodlivost lýkožrouta je úzce svázaná se zdravotním stavem porostů a vhodnými klimatickými podmínkami v daném místě.

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U lýkožrouta smrkového se předpokládá zkrácení doby vývoje, což mu umožní ukončit životní cyklus dříve a založit další generace během sezóny (Lange et al. 2006). Změna klimatu také ovlivní rojení, diapauzu a zimní mortalitu tohoto škůdce. Teplotní režim v průběhu podzimu by pak měl rozhodující vliv na velikost populace během rojení na jaře následujícího roku (Jönsson et al. 2009).

POUŽITÁ DATA A METODY

Analýza vývoje lýkožrouta smrkového byla založena na modelu PHENIPS – Komplexním fenologickém modelu lýkožrouta smrkového *Ips typographus* (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vzduchu den nástupu napadení a průměrná teplota kůry určuje rychlost vývoje jednotlivých vývojových stadií.

Klimatická data byla převzata z databáze FORESEE (Dobor et al. 2012), která obsahuje modifikované výstupy regionálních klimatických simulací provedených v rámci projektu ENSEMBLES (Van der Linden et al. 2009). Data o rozšíření smrku ztepilého v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, prediktivního mapování a národních lesnických statistik (Brus a kol. 2011). Pro účely této práce byly mapy korigovány na základě dat Corine Landcover.

PROCENTUÁLNÍ ZASTOUPENÍ SMRKOVÝCH POROSTŮ V KARPATSKÝCH ZEMÍCH UMOŽŇUJÍCÍ VÝVOJ URČITÉHO POČTU GENERACÍ LÝKOŽROUTA SMRKOVÉHO V OBDOBÍ 1961-1990

Tato mapa byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH91097 „Vyhodnocení dopadu globálních klimatických změn na rozšíření a voltinismus *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) ve smrkových porostech České republiky jako východisko pro jejich trvale udržitelný management.“

PRŮMĚRNÁ ROČNÍ TEPLOTA V OBDOBÍ 1961-1990

POUŽITÁ LITERATURA

Lýkožrout smrkový (***Ips typographus***) v Karpatech: Předpokládaný počet generací za rok v období 2021-2050

Jiří Trombik, Tomáš Hlásny & Jaroslav Holuša

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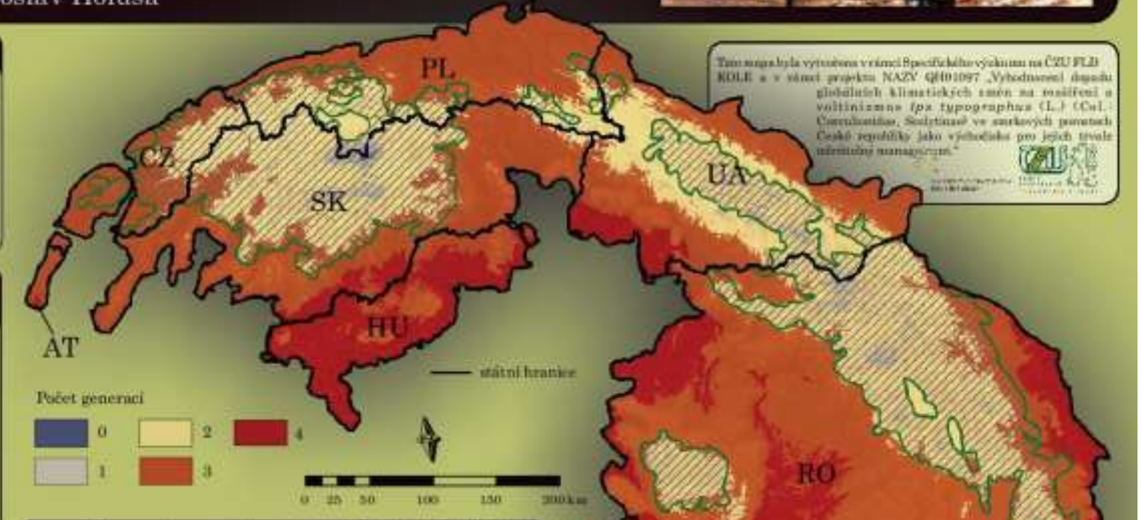
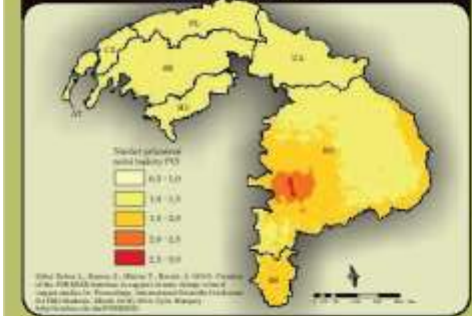


ZMĚNA PRŮMĚRNÉ ROČNÍ TEPLOTY MEZI OBDOBÍMI 1961-1990 A 2021-2050



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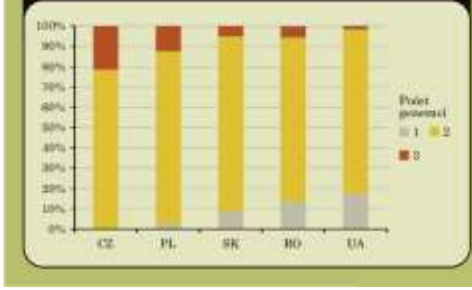
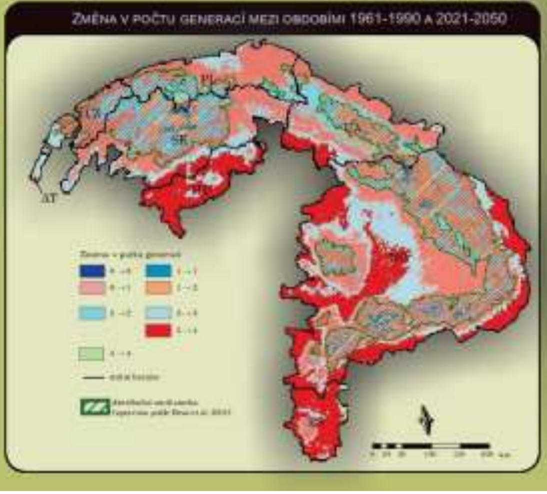
PROCENTUÁLNÍ ZASTOUPENÍ SMRKOVÝCH POROSTŮ V KARPATSKÝCH ZEMÍCH UMOŽŇUJÍCÍ VÝVOJ URČITÉHO POČTU GENERACÍ LÝKOŽROUTA SMRKOVÉHO V OBDOBÍ 2021-2050



ZMĚNA V POČTU GENERACÍ MEZI OBDOBÍMI 1961-1990 A 2021-2050



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BRUS D. J., HENGEVELD G. M., WALVOORT D. J. J., GOEDHART P. W., HEIDEMA A. H., NABUURS G. J., GUNIA K. (2011): [illegible]

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Lýkožrout smrkový (***Ips typographus***) v Karpatech: Předpokládaný počet generací za rok v období 2071-2100

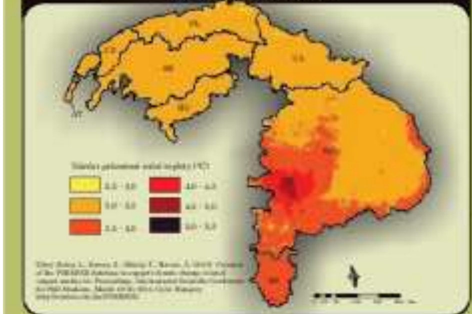
Jiří Trombik, Tomáš Hlásny & Jaroslav Holuša

POUŽITÁ DATA A METODY

Analýza vývoje lýkožrouta smrkového byla založena na modelu PHENIPS – Komplexním fenologickém modelu lýkožrouta smrkového *Ips typographus* (Baier et al. 2007). V rámci tohoto modelu určuje maximální denní teplota vhodného den nástupu napadení a průměrná teplota kůry určuje rychlost vývoje jednotlivých vývojových stadií.

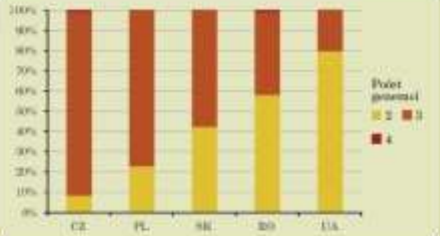
Klimatická data byla převzata z databáze FORESEE (Dobor et al. 2012), která obsahuje modifikované výsledky regionálních klimatických simulací prováděných v rámci projektu ENSEMBLES (Van der Linden et al. 2009). Data o rozšíření smrku ztepilého v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, prediktivního mapování a národních lesnických statistik (Brus a kol. 2011). Pro účely této práce byly mapy korigovány na základě dat Corine Landcover.

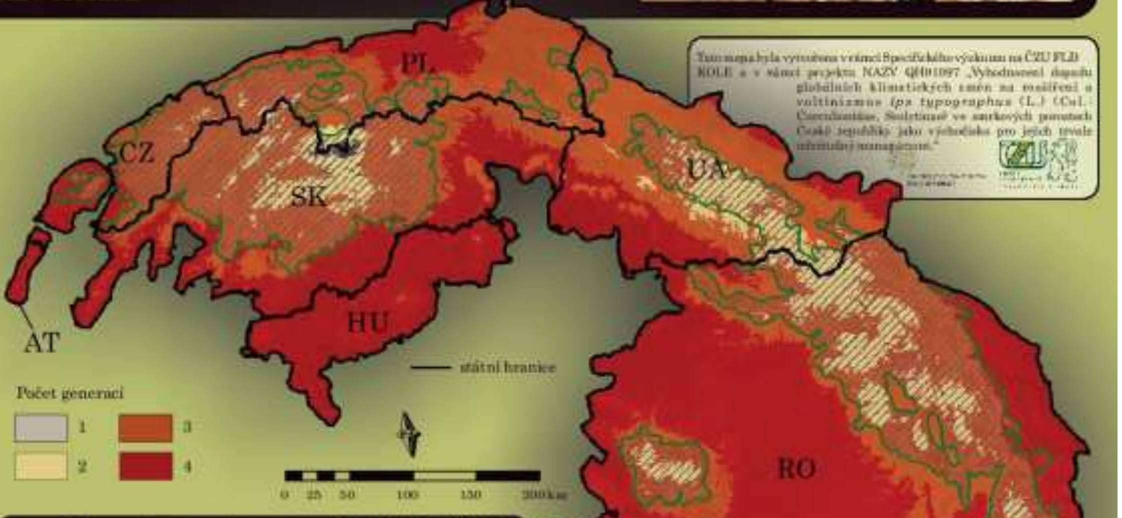
ZMĚNA PRŮMĚRNÉ ROČNÍ TEPLOTY MEZI OBDOBÍMI 1961-1990 A 2071-2100



Zdroj: Dobor L., Barcza Z., Hlásny T., Havasi Á. (2012): [illegible]

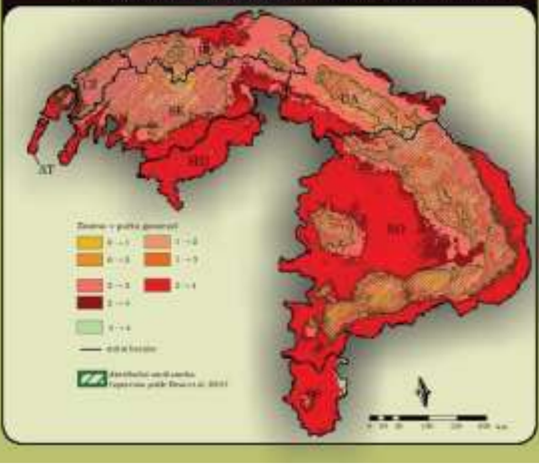
PROCENTUÁLNÍ ZASTOUPENÍ SMRKOVÝCH POROSTŮ V KARPATSKÝCH ZEMÍCH UMOŽŇUJÍCÍ VÝVOJ URČITÉHO POČTU GENERACÍ LÝKOŽROUTA SMRKOVÉHO V OBDOBÍ 2071-2100





Tato mapa byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH91097 „Vyhodnocení dopadu globálních klimatických změn na rozšíření a voltinizmus *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) ve smrkových porostech České republiky jako východisko pro jejich trvale udržitelný management.“

ZMĚNA V POČTU GENERACÍ MEZI OBDOBÍMI 1961-1990 A 2071-2100



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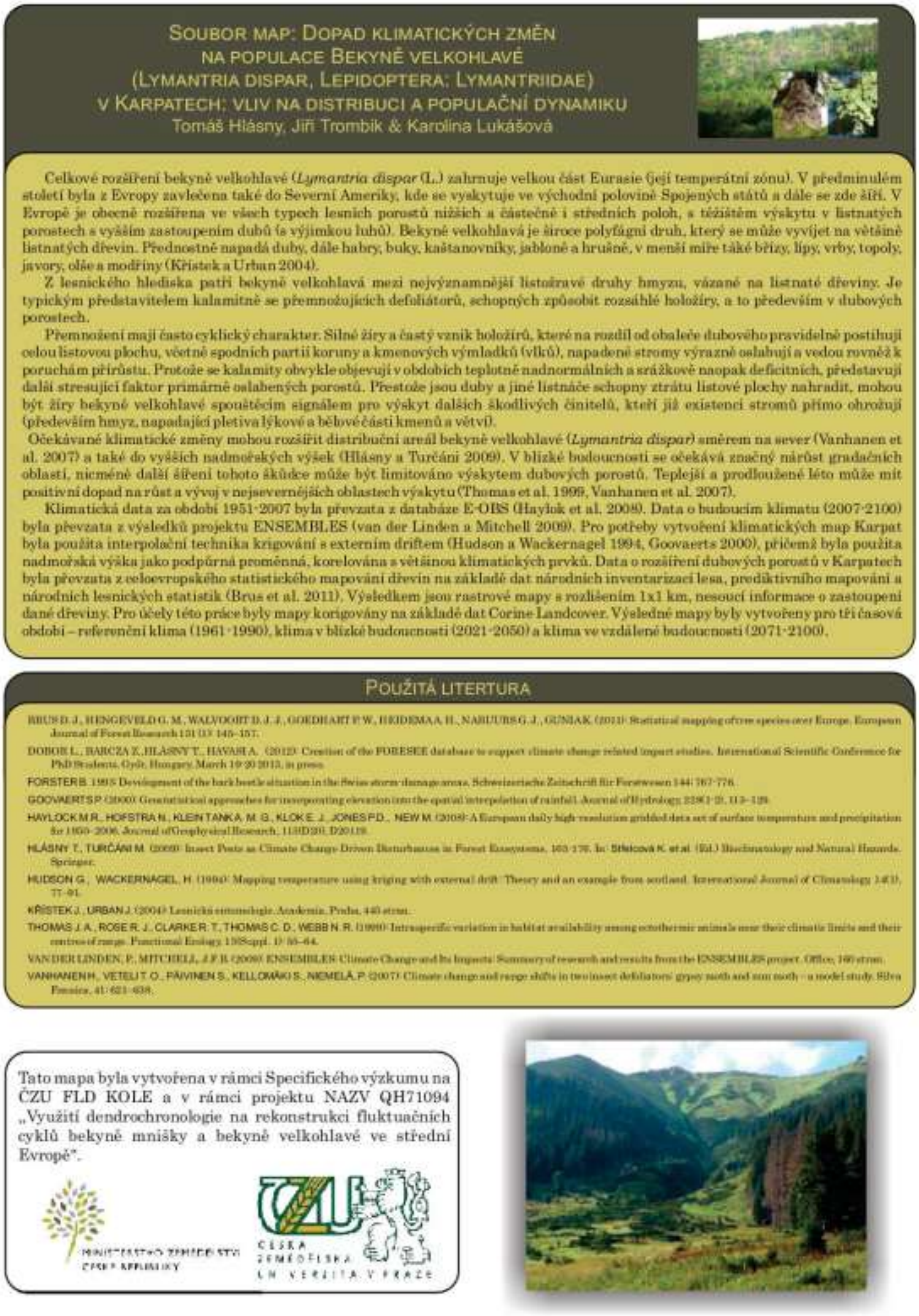
BRUS D. J., HENGEVELD G. M., WALVOORT D. J. J., GOEDHART P. W., HEIDEMA A. H., NABUURS G. J., GUNIA K. (2011): Statistical mapping of tree species over Europe. European Journal of Forest Research 131 (1): 145–157.

DOBOR L., BARCZA Z., HLÁSNY T., HAVASI Á. (2012): Overview of the FORESEE database to support climate change-related impact studies. International Scientific Conference for PhD Students, Győr, Hungary, [illegible]

VAN DER LINDEN P., MITCHELL J. F. B. (2009): ENSEMBLES: Climate Change and its Impacts: Summary of research and results from the ENSEMBLES project. [illegible]

Příloha č.3 Soubor map: Dopad klimatických změn na populace bekyně velkohlavé (*Lymantria dispar* Lepidoptera: Lymantriidae) v Karpatech: Vliv na distribuci a populační dynamiku.



SOUBOR MAP: DOPAD KLIMATICKÝCH ZMĚN NA POPULACE BEKYNĚ VELKOHLAVÉ (LYMANTRIA DISPAR, LEPIDOPTERA: LYMANTRIIDAE) V KARPATECH: VLIV NA DISTRIBUCI A POPULAČNÍ DYNAMIKU

Tomáš Hlásny, Jiří Trombik & Karolina Lukášová

Celkové rozšíření bekyně velkohlavé (*Lymantria dispar* (L.) zahrnuje velkou část Eurasie (její temperátní zónu). V předminulém století byla z Evropy zavlečena také do Severní Ameriky, kde se vyskytuje ve východní polovině Spojených států a dále se zde šíří. V Evropě je obecně rozšířena ve všech typech lesních porostů nižších a částečně i středních poloh, s těžištěm výskytu v listnatých porostech s vyšším zastoupením dubů (s výjimkou luhů). Bekyně velkohlavá je široce polyfágní druh, který se může vyvíjet na většině listnatých dřevin. Přednostně napadá duby, dále habry, buky, kaštanovníky, jabloně a hrušně, v menší míře také břízy, lípy, vrby, topoly, javory, olše a modříny (Křístek a Urban 2004).

Z lesnického hlediska patří bekyně velkohlavá mezi nejvýznamnější listožravé druhy hmyzu, vázané na listnaté dřeviny. Je typickým představitelem kalamitně se přemnožujících defoliátorů, schopných způsobit rozsáhlé holožíry, a to především v dubových porostech.

Přemnožení mají často cyklický charakter. Silné žíry a častý vznik holožírů, které na rozdíl od obaleče dubového pravidelně postihují celou listovou plochu, včetně spodních partií koruny a kmenových výmladků (vlků), napadené stromy výrazně oslabují a vedou rovněž k poruchám přírůstu. Protože se kalamity obvykle objevují v obdobích teplotně nadnormálních a srážkově naopak deficitních, představují další stresující faktor primárně oslabených porostů. Přestože jsou duby a jiné listnáče schopny ztrátu listové plochy nahradit, mohou být žíry bekyně velkohlavé spouštěcím signálem pro výskyt dalších škodlivých činitelů, kteří již existenci stromů přímo ohrožují (především hmyz, napadající pletiva lýkové a bělové části kmenů a větví).

Očekávané klimatické změny mohou rozšířit distribuční areál bekyně velkohlavé (*Lymantria dispar*) směrem na sever (Vanhanen et al. 2007) a také do vyšších nadmořských výšek (Hlásny a Turčáni 2009). V blízké budoucnosti se očekává značný nárůst gradačních oblastí, nicméně další šíření tohoto škůdce může být limitováno výskytem dubových porostů. Teplejší a prodloužené léto může mít positivní dopad na růst a vývoj v nejsevernějších oblastech výskytu (Thomas et al. 1999, Vanhanen et al. 2007).

Klimatická data za období 1951-2007 byla převzata z databáze E-OBS (Haylok et al. 2008). Data o budoucím klimatu (2007-2100) byla převzata z výsledků projektu ENSEMBLES (van der Linden a Mitchell 2009). Pro potřeby vytvoření klimatických map Karpat byla použita interpolační technika krigování s externím driftem (Hudson a Wackernagel 1994, Goovaerts 2000), přičemž byla použita nadmořská výška jako podpůrná proměnná, korelována s většinou klimatických prvků. Data o rozšíření dubových porostů v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, prediktivního mapování a národních lesnických statistik (Brus et al. 2011). Výsledkem jsou rastrové mapy s rozlišením 1x1 km, nesoucí informace o zastoupení dané dřeviny. Pro účely této práce byly mapy korigovány na základě dat Corine Landcover. Výsledné mapy byly vytvořeny pro tři časová období – referenční klima (1961-1990), klima v blízké budoucnosti (2021-2050) a klima ve vzdálené budoucnosti (2071-2100).

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Tato mapa byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH71094 „Využití dendrochronologie na rekonstrukci fluktuačních cyklů bekyně mnišky a bekyně velkohlavé ve střední Evropě".

Bekyně velkohlavá (***Lymantria dispar***) v Karpatech:
Potenciální oblasti gradace v dubových porostech v období 1961-1990

Tomáš Hlásny, Jiří Trombik & Karolina Lukášová

POUŽITÁ DATA A METODY

Změny v potenciálních oblastech přemnožení byly hodnoceny na základě modelu navrženého Hlásnym a Turčánim (2009). Kanonická korespondenční analýza byla použita pro identifikaci environmentálních proměnných kontrolujících abundanci Bekyně velkohlavé. Analýza prokázala pozitivní korelaci s teplotou vzduchu a zastoupením dubu v porostu (Hlásny a Turčáni 2009). Vážený průměr těchto proměnných (ve formě map), přepočtený na škálu 0-1, byl použit pro identifikaci porostů, potenciálně vhodných pro gradaci populací bekyně velkohlavé jak v současném, tak i budoucím klimatu.

Váhy jednotlivých proměnných byly ustanoveny na 0.4 (pro zastoupení dubu) a 0.6 (pro teplotu vzduchu). Tímto způsobem byly získány mapy zobrazující gradační potenciál bekyně na území Karpat, dosahujících hodnot 0-1. Prahová hodnota 0.8 byla použita pro identifikaci potenciálních oblastí gradace.

Klimatická data byla převzata z databáze FORESEE (Dobor et al. 2012), která obsahuje modifikované výstupy regionálních klimatických simulací provedených v rámci projektu ENSEMBLES (Van der Linden et al. 2009). 4 regionální klimatické modely (RKM) byly použity pro simulaci budoucího klimatu - RegCM, HIRHAM, RACMO and REMO. Data o zastoupení dubu v Karpatech byla převzata z celoevropského statistického mapování dřevin na základě dat národních inventarizací lesa, produktivního mapování a národních lesnických statistik (Brus a kol. 2011). Pro účely této práce byly mapy korigovány na základě dat Corine Landcover.

POUŽITÁ LITERATURA

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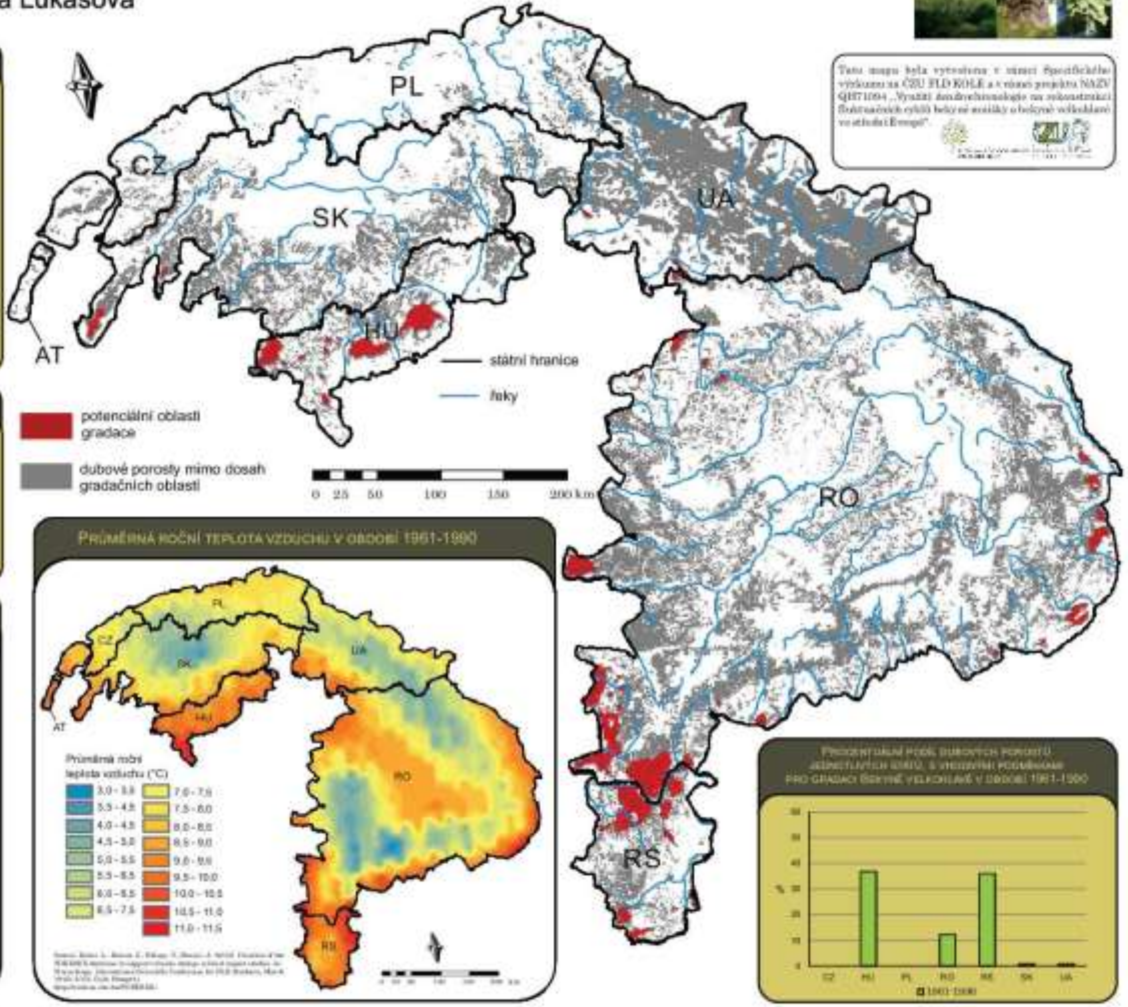
ZASTOUPENÍ DUBU V KARPATECH



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Bekyně velkohlavá (***Lymantria dispar***) v Karpatech:
Potenciální oblasti gradace v dubových porostech v období 2021-2050

Tomáš Hlásny, Jiří Trombik & Karolina Lukášová

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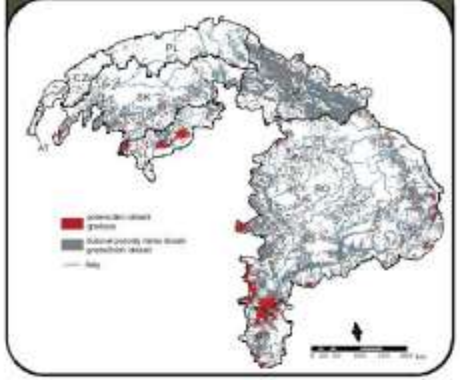
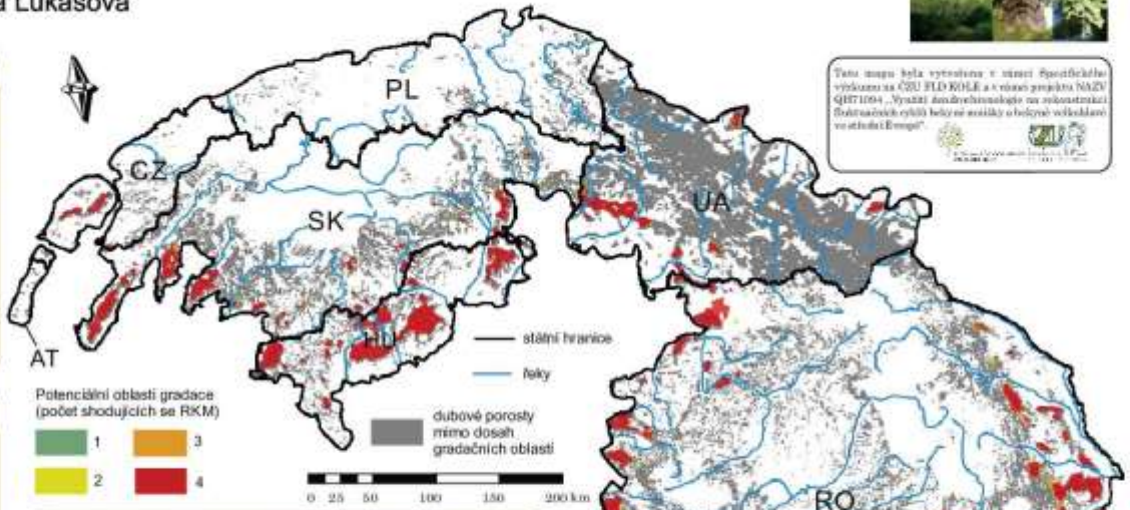
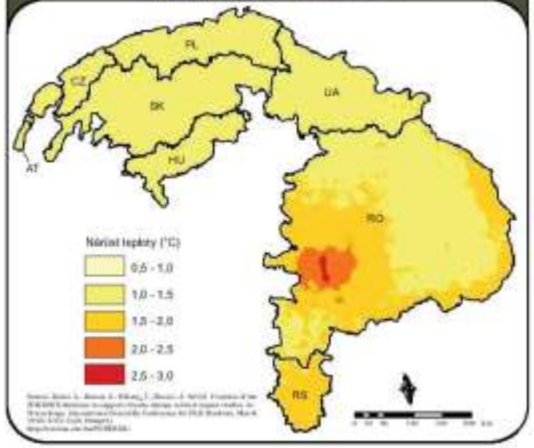
GRADAČNÍ OBLASTI V OBDOBÍ 1961-1990





ZMĚNA PRŮMĚRNÉ ROČNÍ TEPLOTY VZDUCHU MEZI OBDOBÍ 1961-1990 A 2021-2050



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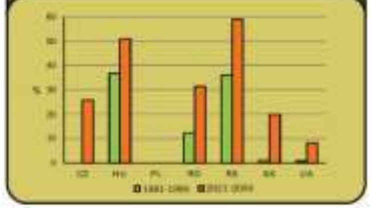
PROCENTUÁLNÍ PODÍL DUBOVÝCH POROSTŮ JEDNOTLIVÝCH STÁTŮ, S VHODNÝMI PODMÍNKAMI PRO GRADACI BEKYNĚ VELKOHLAVÉ V OBDOBÍ 2021-2050



Bekyně velkohlavá (***Lymantria dispar***) v Karpatech:
Potenciální oblasti gradace v dubových porostech v období 2071-2100

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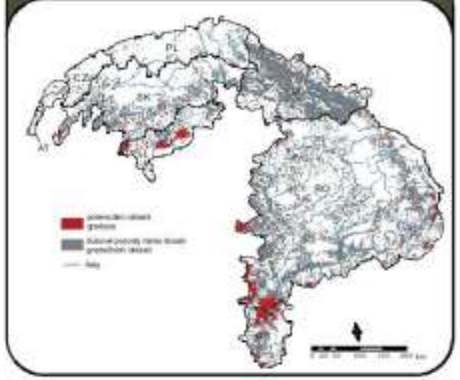
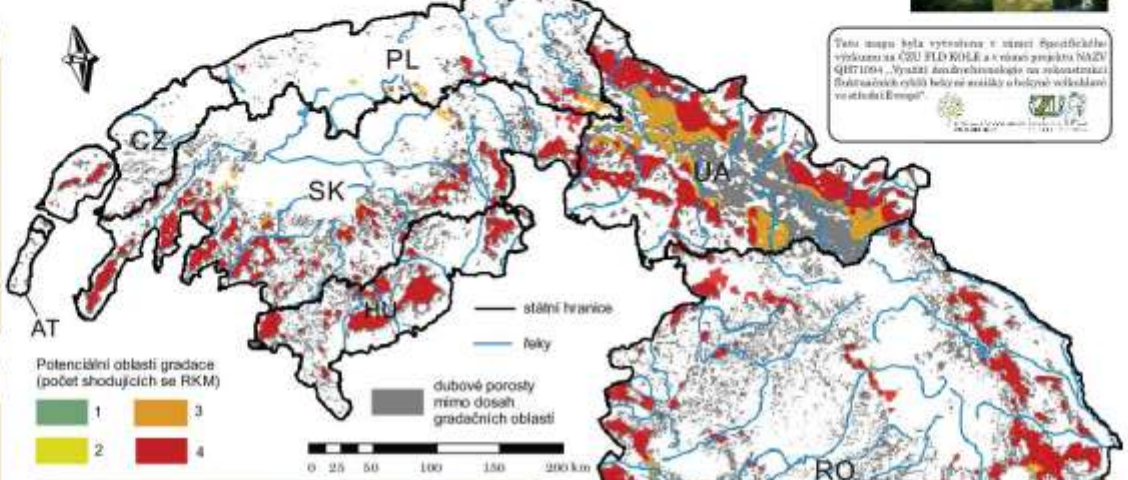
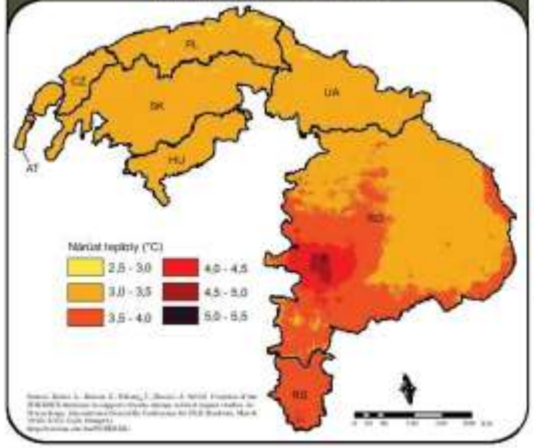




ZMĚNA PRŮMĚRNÉ ROČNÍ TEPLOTY VZDUCHU MEZI OBDOBÍ 1961-1990 A 2071-2100



Tato mapa byla vytvořena v rámci Specifického výzkumu na ČZU FLD KOLE a v rámci projektu NAZV QH71094 „Využití dendrochronologie na rekonstrukci fluktuačních cyklů bekyně mniškové a bekyně velkohlavé ve střední Evropě".

PROCENTUÁLNÍ PODÍL DUBOVÝCH POROSTŮ JEDNOTLIVÝCH STÁTŮ, S VHODNÝMI PODMÍNKAMI PRO GRADACI BEKYNĚ VELKOHLAVÉ V OBDOBÍ 2071-2100