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Hodnocení účinnosti a vedlejších dopadů managementu kůrovce v podmínkách změny klimatu

Disertační práce

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Evaluation of efficiency and collateral effects of bark beetle management under climate change

Ph.D. Thesis

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"Prohlašuji, že jsem disertační práci na téma Hodnocení účinnosti a vedlejších dopadů managementu kůrovce v podmínkách změny klimatu vypracovala samostatně s použitím uvedené literatury a na základě konzultací a doporučení školitele.

Souhlasím se zveřejněním disertační práce dle zákona č. 111/1998 Sb. o vysokých školách v platném znění, a to bez ohledu na výsledek její obhajoby."

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Podpis autora

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Abstrakt

Lesní ekosystémy střední Evropy jsou několik posledních desetiletí pod tlakem sílících přemnožení kůrovců. Přemnožení kůrovců jsou nejčastěji vyvolávána častějším výskytem větrných disturbancí či období sucha, které jsou v mnoha případech spouštěcím mechanismem pro rozvoj populace. Tyto mechanismy a kalamitní stav, v němž se smrkové porosty ocitly, jsou z velké části výsledkem působení změny klimatu. Jelikož klimatická změna bude v budoucnu ještě intenzivnější, je třeba přehodnotit stávající postupy managementu přemnožení kůrovců. Výzkum by měl vyhledávat inovativní a efektivnější způsoby, jak disturbance lépe zvládat, zmírňovat jejich dopady nebo s nimi při hospodaření přímo počítat. Předložená disertační práce se zaměřuje na rozšíření poznatků o vybraných nástrojích managementu kůrovcových disturbancí, zhodnocení jejich účinnosti a jejich možných vedlejších vlivů na lesní ekosystémy. Práce je složena ze 4 studií zaměřených na management přemnožení kůrovců, které se opírají o využití procesního modelu iLand. Závěry těchto studií jsou podpořeny výsledky dalšího výzkumu, na kterém se autorka podílela, jenž byl zaměřen na rozšíření obecných poznatků o populační dynamice kůrovců a dopadů jejich přemnožení.

Studie Zimová et al. (2020) hodnotí vliv zkracování doby obmýtí jako nástroje pro snižování rizika vniku poškození porostů větrem a kůrovcem. Výsledky ukazují, že tento přístup snižuje riziko disturbancí jak kůrovcových, tak větrných, avšak v podmínkách změny klimatu jeho účinnost klesá. Zkracování doby obmýtí také krátkodobě snižuje zásoby uhlíku v lese a může mít negativní dopady na ukazatele biodiversity, zejména z důvodu snížení početnosti dospělých stromů, které jsou důležitým habitatem pro řadu druhů.

Studie Dobor et al. (2019) a Dobor et al. (2020a) se zaměřily na efektivitu nahodilé těžby větrem poškozených stromů vzhledem ke vzniku a průběhu přemnožení kůrovců. Testovaná byla jak různá intenzita prováděných zásahů, tak i jejich prostorové rozmístění. Simulace prokázaly, že nahodilá těžba je efektivním nástrojem pro prevenci nebo potlačení přemnožení pouze je-li prováděna ve vysokých intenzitách. Obdobně jako v případě snížení doby obmýtí, i zde se účinnost výrazně snížila vlivem teplejšího klimatu. Nahodilá těžba neměla výrazný účinek na celkový uhlík v lese. Hladina uhlíku odstraněného těžbou ven z lesa a uhlíku v živých stromech, které byly ušetřeny před dopady disturbance, se vzájemně kompenzovaly. Celkové množství uhlíku v lese bylo více zasaženo změnou klimatu než uvedeným managementem. Na rozdíl od toho nahodilá těžba zapříčinila zvyšování uhlíku uloženého v živých stromech.

Shrnutím a rozšířením předchozích podkladů je studie Dobor et al. (2020b) věnující se hodnocení kombinovaného vlivu nahodilých těžeb a snížení obmýtí s cílenou změnou dřevinné skladby. Výsledky prokázaly, že změna klimatu zvětšuje rozdíly mezi zranitelností stejnorodých a druhově pestrých porostů ve prospěch pestrých porostů. Naopak, management zaměřený na udržení převážně smrkových porostů nebyl udržitelný ani při vysoké intenzitě nahodilých těžeb a výrazném snížení obmýtí. Změna dřevinné skladby byla prospěšná nejen z hlediska snížení vlivu disturbancí ale i z hlediska zásob uhlíku v lese a různých ukazatelů biodiverzity.

Předešlé studie jsou doplněny o podrobné zhodnocení příčin a dopadů kůrovcové kalamity v České republice (Hlásny et al. 2021) a o příspěvek k empirickému výzkumu populační dynamiky kůrovců (Zimová et al. 2019).

Prezentované výsledky poukazují na skutečnost, že stávající postupy managementu disturbancí nebudou v podmínkách změny klimatu dostačující a vyžadují revizi. Předložená disertační práce je důležitým příspěvkem k problematice managementu kůrovcových disturbancí v podmínkách změny klimatu. V dalším období by tyto výsledky měly být zohledněny v praktické ochraně lesa i vzdělávání.

Klíčová slova: gradace lýkožrouta, klimatické faktory, ochrana lesa, nahodilé těžby

Abstract

Forest ecosystems of central Europe have been under pressure from bark beetle disturbances for the last few decades. More frequent windthrows and droughts were increasing triggering bark beetle epidemics. This disturbance intensification was caused, to a large extent, by climate change, which accelerates bark beetle development and compromises the defence of host trees. Therefore, bark beetle disturbance management needs to be revised, as climate change will continue to intensify in the future. Research should endeavour to search for innovative and more effective ways of managing disturbances, mitigating their impacts, and incorporating them into management planning. This thesis aims to expand the knowledge about selected measures and strategies for bark beetle disturbance management, evaluate their effectiveness and possible collateral effects on forest ecosystems. The thesis consists of four publications focused on managing bark beetle disturbances conducted using the process-based landscape-scale model iLand. These studies are further supported by additional research papers focused on different aspects of bark beetle population dynamics and impacts on forest ecosystems.

The study by Zimová et al. (2020) assesses the effect of reducing the rotation period as a tool for reducing the risk of bark beetle and wind damage. The results show that this approach reduces the risk of both bark beetle and wind disturbances, but this effect decreases under climate change. Shortening the rotation period also reduces forest carbon stocks, mainly in the short term, and negatively affects some biodiversity indicators, such as the abundance of large habitat trees.

The studies Dobor et al. (2019) and Dobor et al. (2020a) focus on the efficiency of salvage logging of wind-damaged trees and bark beetle outbreaks dynamics. Different intensities and spatial distributions of salvage logging were tested. Simulations have shown that salvage logging is an effective tool for preventing or suppressing outbreaks only if carried out at high intensities. The efficiency decreased significantly under climate change, as in the case of reducing the rotation period. Salvage logging did not have a significant effect on the total carbon in the forest. The levels of carbon removed from forest by logging and the carbon in living trees that were not affected by the disturbance compensated each other.

An extension of the previous studies was the study Dobor et al. (2020b). It evaluated the combined impact of salvage logging, reduced rotation period, and adaptive changes in tree species composition. The results showed that climate change increases differences between the vulnerability of homogenous and species-diverse stands, favouring more diverse stands. On the contrary, management aiming at maintaining predominantly spruce stands was not sustainable even with the high intensity of salvage logging and significant rotation period reduction. The change in tree composition was beneficial not only in reducing the impact of disturbances but also in terms of carbon stocks and various biodiversity indicators.

The previous studies are supported by the detailed evaluation of the causes and impacts of the bark beetle outbreaks in the Czech Republic (Hlásny et al., 2021) and by the empirical research on bark beetle population dynamics (Zimová et al., 2019).

The presented results show that the current bark beetle management practices will not be sufficient to face bark beetle outbreaks amplified by climate change and require fundamental revision. Particularly the combination of silviculture approaches to risk management with traditional bark beetle management strategies should receive increased attention in the future. The research presented in this thesis is essential contribution to bark beetle disturbance management in climate change conditions. The results can be used in practical forest protection and education.

Keywords: bark beetle outbreak, climatic factors, forest protection, salvage logging

Obsah

1 Úvod

Lesní ekosystémy jsou vysoce ohroženy probíhající změnou klimatu. Předpokládá se, že v budoucnu s častěji se vyskytujícími klimatickými extrémy se porosty budou muset vyrovnat s drastickou změnou přírodních podmínek stanovišť (Kolström et al., 2011). Lesní porosty jsou však vzhledem k jejich dlouhodobému vývoji velmi citlivé na rychle se měnící podmínky a stávají se tak velmi zranitelnými. Extrémní podmínky (např. sucho, větrné disturbance a následné gradace kůrovce) ohrožují ekosystémové služby a funkce, které les poskytuje (Lenton et al., 2008).

Klimatická změna má vliv na množství různých ekosystémů a její vývoj je ovlivněn lidskou činností (Turner et al., 2020). Ke stavu klimatu přispívají antropogenní změny krajiny, jako jsou změny ve vodním režimu, intenzivní zemědělství či stále vyšší procento zastavěných ploch. Jedním z hlavních faktorů ovlivňujících klimatickou změnu je však zvyšující se stav koncentrací skleníkových plynů (Nitschke and Innes, 2008). Důsledky skleníkového efektu se projevují především změnou srážkového režimu a nárůstem teplot vzduchu, které současně způsobují nedostatek vody a častější extrémní sucha. Tyto jevy mají vliv na vývoj a mortalitu lesních ekosystémů. Jak roste intenzita sucha, roste současně mortalita stromů, snižuje se ukládání uhlíku v lese a zvyšuje se výskyt požárů (Hanewinkel et al., 2013; Turner et al., 2020). Nejnovější výzkumy ukazují, že v mnoha regionech budou klimatické extrémy častější, delší a jejich průběh intenzivnější (Turner et al., 2020). Podmínky klimatu budou snižovat obranyschopnost stávajících lesních porostů, které tak budou nadále vystaveny disturbancím a nebudou tak poskytovat ekosystémové služby v původním rozsahu. (Cook et al., 2018; Jönsson et al., 2009; Morris et al., 2018; Seidl et al., 2017).

Ekosystémové procesy jsou nejčastěji narušovány činiteli jako je vítr, kůrovec a požáry. (Lindroth et al., 2009; Seidl et al., 2014b). Frekvence jejich výskytu v současné době velmi rychle nabírá na intenzitě a narůstá zájem o jejich management (Seidl et al., 2017, 2011b; Turner, 2010). Disturbanční činitelé na sobě bývají často prostorově a časově závislí. Jako příklad lze uvést zřejmé propojení mezi větrnými a následnými kůrovcovými disturbancemi (Stadelmann et al., 2014), stejně tak jako mezi kůrovcovými disturbancemi a suchem (Seidl et al., 2016). Lesní ekosystémy jsou silně zasaženy disturbancemi a klima zřejmě v tomto ohledu má klíčovou roli, která mimo jiné spočívá i ve vlivu klimatických změn na populační dynamiku kůrovců, kteří jsou na změny teplot vysoce citliví (Bentz et al., 2019; Cudmore et al., 2010). Jejich masové šíření následující větrné disturbance nebo období sucha je závažným problémem ohrožujícím vyspělé převážně smrkové porosty (Jönsson et al., 2007; Wermelinger, 2004).

Zintenzivňující se gradace kůrovců posledních několika desetiletí přispěly k zdvojnásobení mortality porostů střední Evropy (Seidl et al., 2014b; Senf et al., 2018). V porovnání s obdobím 1971–1980 se předpokládá, že vlivem klimatické změny bude do roku 2030 kůrovcová disturbance sedminásobná (Seidl et al., 2014b). Česká republika se stala epicentrem kůrovcového ohniska ve střední Evropě (Hlásny et al., 2021). Poslední roky zde objem těžby smrkového dříví poškozeného kůrovcem dosahuje desítek milionů kubických metrů ročně a v historickém kontextu tak nyní čelíme největšímu přemnožení smrkových kůrovců (Hlásny et al., 2021; Ministry of Agriculture of the Czech Republic, 2020).

Přírodní disturbance mají v utváření dynamiky lesní krajiny, ve struktuře a fungování ekosystému klíčovou roli. Jsou přirozenou součástí koloběhu živin. Díky přítomnosti mrtvého dřeva a množství světla dopadajícího na půdu zvyšují diverzitu stanovištních podmínek a s tím roste i biodiverzita (Turner et al., 2004). V některých případech se její úroveň po zasažení disturbancí může rovnat i pralesním ekosystémům. Často se na takových stanovištích objevují i zákonem chráněné druhy rostlin i živočichů. Působením disturbancí ani výrazně netrpí kvalita vody. Snížením transpirace a změnou vsakování se však po určitou dobu změní její distribuce v krajině. Nové podmínky vzniklé působením disturbance mohou mít někdy pozitivní vliv na zdravotní stav porostů a jejich produkci (Beudert et al., 2015).

V hospodářských lesích se však disturbance projevují převážně jako negativní faktory, které budou mít v budoucnu díky působení změny klimatu stále závažnější průběh a dopad na lesní hospodářství (Lindroth et al., 2009; Seidl et al., 2014b; Seidl and Blennow, 2012). Smrk je hlavní hospodářskou dřevinou v mnoha státech. Jeho ohrožení disturbancemi může mít dopad na ekonomiku celého lesnického sektoru a ovlivnit světové trhy se dřevem (Grégoire et al., 2015; Montagné-Huck and Brunette, 2018). Disturbance ohrožují také ekosystémové služby. Jedná se o služby jak regulační, tak kulturní, mezi nimi například problematika uložení uhlíku, biodiverzita, ale také rekreace a estetická hodnota lesa (Dobor et al., 2018; Thom and Seidl, 2016).

Nedílnou součástí lesního hospodaření v Evropě je snaha o předcházení disturbancím nebo alespoň zmírnění jejich dopadů. Management se zaměřuje buď na přímou kontrolu populací kůrovce nebo na vytváření porostů odolnějších negativním podmínkám (Wermelinger, 2004). Cílem přímých metod managementu je snižovat populace kůrovců za pomoci odchytových zařízení a insekticidních přípravků a také zamezovat přítomnosti materiálu vhodného k rozmnožování imag za pomoci jeho odstraňování z porostu (Faccoli and Stergulc, 2008; Stadelmann et al., 2013). Naopak, nepřímý management má za cíl například zlepšování vitality stromů, snižování zastoupení hostitelských dřevin a zranitelných věkových stadií, snižování konektivity velkých celků hostitelských dřevin apod. K tomu slouží například probírky, změny těžební úpravy nebo volba vhodné dřevinné skladby, které mají za úkol diverzifikovat porosty (Fettig and Hilszczański, 2015). Aby se zamezilo šíření kůrovce, je vhodné orientovat management nejen na úroveň porostů ale i na úroveň krajiny. Úspěchy managementu lokálních ohnisek jednotlivých porostů nemusí mít výrazný vliv na dynamiku kůrovce na úrovni krajiny a mohou zkreslovat účinnost opatření. Je tedy třeba důrazně sledovat dopady provedeného managementu na okolní porosty a provádět opatření komplexně ve větším měřítku s dosahem na celou krajinu (Björkman et al., 2015; Honkaniemi et al., 2020; Jactel et al., 2009).

Výzkumu managementu disturbancí lesních ekosystémů se již věnovalo mnoho studií. I přesto zůstávají některé zákonitosti vztahů managementu lesa, jeho vlivu na dynamiku disturbancí, dopady na ekosystémové služby a interakce se změnou klimatu nedostatečně objasněné (Hlásny et al., 2019; Kausrud et al., 2012). Intenzivní výskyt disturbancí a jejich dopad na ekosystémové služby zdůrazňuje potřebu zkvalitnění managementu (Senf et al., 2018). V rámci změny klimatu se situace bude nadále zhoršovat a proto jsou revize stávajících opatření a hledání nových řešení nevyhnutelné (Hlásny et al., 2019; Honkaniemi et al., 2020; Seidl et al., 2018). Další výzkum by se měl zaměřovat na kvantitativní pochopení dopadů interakcí různých opatření managementu. Je třeba zohlednit možnost změny porostní skladby vstříc diverzifikovaným porostům, která může být prováděna za současného využití dalších opatření jako je nahodilá těžba, odchyt kůrovců či předmýtní těžba na ohrožených stanovištích. Interakce těchto postupů však mohou vést k nepředpokládaným účinkům na procesy v lesním ekosystému. Vztahy ekosystémů postižených disturbancí s managementem mohou být ovlivněny klimatickou změnou a jejím působením budou modifikovány i jednotlivé dopady (Dobor et al., 2020b, 2019; Zimová et al., 2020).

Tato práce je snahou o ucelení a prohloubení poznatků o možnostech managementu kůrovcových disturbancí, jejich efektivitě a zhodnocení možností budoucího hospodaření v lesích střední Evropy v podmínkách změny klimatu.

2 Cíle práce

Cílem této práce je kvantifikovat účinnost opatření zaměřených na snižování rizika vzniku a dopadů přemnožení kůrovce na lesy, vliv vzájemné interakce těchto postupů a zhodnotit případné změny jejich účinnosti v důsledku změny klimatu, která ovlivňuje jak vývoj kůrovce, tak i kondici stromů. V souladu se zadáním dizertační práce řešení sestává z několika případových studí opírajících se převážně o využití procesního modelu iLand. Doplněním jsou zde některé poznatky z empirického výzkumu prohlubující problematiku populační dynamiky kůrovců. V práci jsou na základě výsledků formulována doporučení budoucího managementu kůrovcových disturbancí za podmínek změny klimatu.

Cíle práce byly dosaženy v rámci šesti vědeckých publikací uveřejněných v časopisech s impakt faktorem. Cíle a hypotézy, o které se jednotlivé studie při řešení opíraly, jsou následující:

Dílčí cíl 1: Vyhodnotit vliv zkrácení doby obmýtí na míru poškozování porostů větrem a kůrovcem. Cílem je testovat několik intenzit relativního zkrácený doby obmýtí a vývoj ovlivněný změnou klimatu. Zároveň bude hodnocen dopad na uhlík a ukazatele biodiverzity prostředí. Hypotézou je, že zkrácení doby obmýtí povede ke snížení množství vhodného hostitelského materiálu a následně tak k redukci škod způsobených kůrovcem. Tento efekt však může být negativně ovlivněn změnou klimatu. Předpokládá se, že zvolený management, bude mít krátkodobý negativní dopad na množství uhlíku v prostředí a podepíše se i na stavu ukazatelů biodiverzity.

Dílčí cíl 2: Vyhodnotit vliv různé intenzity odstraňování větrem poškozených stromů na průběh přemnožení kůrovce a na zásoby uhlíku v lesním ekosystému. Tento cíl se tedy zaměřuje na vyhodnocení možných vedlejších nepříznivých dopadů nahodilých těžeb. Hypotézou je, že prevence vzniku přemnožení kůrovců v podobě odstraňování větrem poškozených stromů zmírní průběh přemnožení a zvýší objem uhlíku v živých stromech. Z hlediska celkové zásoby uhlíku v ekosystému, do které spadá i mrtvé dřevo, je však výsledný efekt nejasný.

Dílčí cíl 3: Vyhodnotit vliv různé intenzity a prostorového uspořádání odstraňování větrem poškozených stromů na míru škod způsobených kůrovcem. Testován je vliv plošného odstraňování poškozených stromů s různou intenzitou, odstraňování stromů pouze v okolí cest a odstraňování stromů v souvislých částech území, které mohou reprezentovat například bezzásahové plochy. Naše hypotézy jsou, že odstraňování poškozených stromů povede ke snížení dopadů kůrovcových disturbancí. Umístění těžby v okolí cest by mohlo být efektivní pro zpomalení postupu kůrovce porostem. Bezzásahová území nemusí mít negativní vliv na ostatní území, při důsledném provádění odstraňování materiálu z oblastí s možností zásahu. Dále se předpokládá, že změna klimatu sníží účinnost všech testovaných variant z důvodu urychleného vývoje kůrovců a oslabení obranných mechanismů stromů.

Dílčí cíl 4: Vyhodnotit interakci managementových opatření v podobě odstraňování poškozených stromů, zkrácení doby obmýtí a postupné změny dřevinné skladby. Cílem je otestovat rozdílné intenzity a kombinace uvedených opatření, jejich interakce a dopady na škody způsobené kůrovcem. Předpokladem je, že intenzivní odstraňování poškozených stromů a postupné snižování věku porostů, způsobené zkrácenou dobou obmýtí, povede ke snížení dopadů kůrovcových disturbancí. Diferenciace porostu změnou skladby dřevin povede ke snížení dostupnosti hostitelského materiálu, a tak následnému omezení dopadů kůrovce.

Kromě výše uvedených cílů zaměřených na optimalizaci postupů managementu lesa, byly v rámci disertační práce provedeny další dvě podpůrné studie, které vhodným způsobem doplňují studie opírající se o modelování. Cíli těchto studií bylo:

- Shrnout a zhodnotit vývoj kůrovcové disturbance na území České republiky. Zhodnotit přímé dopady disturbance na lesnický sektor i v oblasti problematiky sociální, ekonomické a ekologické. Nastínit možný další vývoj kůrovcové problematiky.
- Rozšířit poznatky populační dynamiky kůrovců a mechanizmů jejich šíření do nových oblastí výskytu.

3 Rozbor problematiky

Kůrovci jsou nejdůležitějším biotickým disturbančním faktorem ovlivňujícím mírné a boreální lesní ekosystémy. Obranné mechanismy hostitelského stromu i vývoj samotných kůrovců jsou proměnné silně závislé na klimatických faktorech a reagují tedy velmi citlivě na změny klimatu (Netherer and Schopf, 2010). V současné době lze také v důsledku toho pozorovat zvětšující se a nově vznikající kůrovcová ohniska, mnohdy však situace vede již k rozpadu lesa na krajinné úrovni (Grodzki, 2010; Hlásny and Sitková, 2010). Ve střední Evropě a Severní Americe, jako výsledek reakcí kůrovců na již probíhající klimatické změny, původní druhy kůrovců, jako např. *Ips typographus* (Linnaeus, 1758) v Evropě a *Dendroctonus ponderosae* (Hopkins, 1902) v Americe, napadly porosty na desítkách milionů hektarů a šíří se dál (Bentz et al., 2010; Dobor et al., 2020b; Raffa et al., 2008). Mortalita porostů v Evropě se za posledních 30 let zdvojnásobila (Senf et al., 2018) a jedním z důležitých faktorů je to, že dopady kůrovcových disturbancí se zároveň zvýšily o 60 % (Seidl et al., 2014b).

V Evropě mezi nejvýznamnější škůdce jehličnatých porostů patří lýkožrouti rodu *Ips* (Holuša et al., 2003). Nejrozšířenějším druhem je *Ips typographus*, který svým výskytem silně koresponduje se svojí hostitelskou dřevinou smrkem ztepilým [*Picea abies* (L.) H. Karst.]. Smrk se řadí mezi nejrozšířenější dřeviny střední a severní Evropy (Jönsson et al., 2012). Je jednou z nejvíce hospodářsky ceněných dřevin ve střední Evropě ať už vzhledem ke svému růstovému potenciálu, nízkým kvalitativním požadavkům na lokalitu růstu, snadným využitím nebo dobrou kvalitou dřeva. V České republice zastoupení smrku stále dosahuje více jak 50 % a v důsledku klimatu je jednou z nejohroženějších dřevin (Hanewinkel et al., 2013). Na tomto faktu se podílí také jeho časté vysazovaní mimo přirozený areál výskytu, kde je jeho odolnost a adaptační schopnost snížena (Klimo et al., 2000). *Ips typographus* k náletu upřednostňuje vyspělé smrky ve věku 60 let a více s průměrem ve výčetní tloušťce nad 20 cm. Avšak ve vyšších populačních hustotách může napadnout i stromy mladší a s menším průměrem (Jactel et al., 2009).

Mezi několik dalších druhů kůrovců, kteří ohrožují smrkové porosty spolu s lýkožroutem smrkovým, jejichž výskyt se často prostorově překrývá, patří lýkožrout severský *Ips duplicatus* (Sahlberg, 1836), jehož význam v posledních letech rychle narůstá, lýkožrout menší *Ips amitinus* (Eichhoff, 1871) a lýkožrout lesklý *Pityogenes chalcographus* (Linnaeus, 1761) (Grodzki, 2007; Holuša and Liška, 2002). Tato práce se zaměřuje především na druh *Ips typographus* avšak šetření jednotlivých studií a závěry jsou stavěny tak, že mohou být obecně vztaženy na více druhů kůrovců.

3.1 Mechanismy ovlivňující populační dynamiku kůrovců

Mechanismy ovlivňující populační dynamiku kůrovců mohou mít různé způsoby dělení podle náhledu na problematiku. Například dle původu na biotické a abiotické faktory (Marini et al., 2013) nebo na mechanismy závislé na hustotě (např. populační hustota, míra přemnožení) a na hustotě nezávislé (např. klimatické faktory jako je teplota, srážky či výskyt silného větru či potravinové zdroje) (Marini et al., 2017; Stiling, 1988). V této kapitole jsou faktory ovlivňující dynamiku kůrovců rozděleny na spouštěcí mechanismy a mechanismy přispívající k ukončení gradací.

K úspěšné kolonizaci hostitelského stromu vede komplexní interakce mezi množstvím dospělců, fyziologií dřevin a jejich schopností obrany. Iniciace procesu kolonizace může vzniknout na základě množství spouštěcích mechanismů. Takovýmto významným spouštěcím mechanismem je vítr (Eriksson et al., 2005). Ve většině případů se kůrovcová ohniska zprvu objevují v regionech zasažených bouří s větrem o vysokých rychlostech, odkud se pak dále šíří (Marini et al., 2017). Smrk ztepilý je v porovnání s jinými druhy málo odolný větru (Schmidt et al., 2010). Je také hlavní hostitelskou dřevinou lýkožrouta smrkového a jeho porosty se tak po zásahu větrem stávají vhodným zdrojem k šíření kůrovců (Wermelinger, 2004). Větrem zasažené stromy s nízkou nebo chybějící rezistencí mohou být velmi snadno kolonizovány. Díky velkému množství vhodného materiálu se tak děje často v nízkých hustotách a je tak snížena přirozená kompetice o zdroje (Christiansen and Bakke, 1988; Schroeder, 2010). Větrná disturbance se tak stává ohniskem šíření kůrovců, což vede až k poškozování zdravých stromů (Eriksson et al., 2005). Jako příklad zde může sloužit gradace kůrovců v Bavorském lese po zásazích větrem v letech 1983 a 1984, kdy bylo poškozené dřevo ponecháno v porostu a tento postup vedl k intenzivnímu šíření kůrovců napříč parkem a poškozování zdravých porostů (Heurich et al., 2001; Lausch et al., 2013). Stejným způsobem můžeme pozorovat změnu krajinného rázu Tater, které podléhají posledních 200 let masivní destrukci porostů způsobené frekventovanými zásahy větru (Fleischer et al., 2017). V souvislosti s klimatickou změnou se předpokládá, že interakce mezi kůrovcem a větrnou disturbancí se bude zintenzivňovat (Seidl and Rammer, 2017).

Riziko napadení smrkových porostů kůrovci není spojeno pouze umístěním blízko již existujícímu kůrovcovému ohnisku. Vznik velkých gradací a ohnisek žíru záleží také na hustotě populace imag, ale především na odolnosti jednotlivých stromů. Nicméně za epidemických podmínek bylo 90 % nových ohnisek nalezeno v oblastech vzdálených do 100 m od původního nálezu (Wichmann and Ravn, 2001). K rychlému šíření disturbancí dochází v důsledku poškození porostů větrem, přičemž často přispívá také nedostatečné či pomalé zpracování (Marini et al., 2017; Wermelinger, 2004). Potterf and Bone (2017) prokázali nelineární vztah mezi rozsahem větrných disturbancí a růstem populací kůrovců. Vysoká atraktivita velkých oblastí zasažených větrem může omezit disperzi kůrovců v dané lokalitě vzhledem k množství hostitelského materiálu. Kůrovec tak po nějakou dobu nevyhledává vzdálené atraktivní stromy a nešíří se hned do nových menších ohnisek zásahu větrem. Současná praxe tak doporučuje zaměřit se v první řadě na zpracování menších zásahů větrnou disturbancí, avšak velké oblasti musí být později také zpracovány před dokončením vývoje kůrovců. Studie účinnosti těchto postupů však často nejsou příliš průkazné (Stadelmann et al., 2013).

Dalšími faktory, které ovlivňují vývoj a šíření kůrovců mohou být nadprůměrné teploty a dlouhá období sucha spojená s nedostatečným zásobováním vodou (Marini et al., 2017; Wermelinger, 2004). V minulosti bylo sucho spíše faktorem, který přispíval ke zhoršení situace kůrovcových disturbancí, pouze velmi výjimečně byl primárním spouštěčem (Rouault et al., 2006). Změna klimatu však zvyšuje rizika výskytu sucha. To se pak v kombinaci s vysokými teplotami může stát častěji samostatným spouštěcím mechanismem kůrovcové disturbance (Bentz et al., 2019; Hlásny et al., 2014; Netherer et al., 2019). Klimatická změna navíc zapříčiňuje synchronizaci přemnožení kůrovců, která zasahují větší území (Senf and Seidl, 2018). Spíše v minulosti mohli k rozvoji gradací přispět i porosty zasažené silným znečištěním ovzduší, kupříkladu Beskydy v 70. a 80. letech (Hlásny and Sitková, 2010).

Na rozdíl od spouštěcích mechanismů, procesy, které vedou k ukončování gradací, nejsou doposud dostatečně známé a jejich problematice se věnuje jen omezený počet studií. Za kolaps gradací je označován stav, kdy populace kůrovců dosáhnou tak nízkých počtů, že nejsou schopny odolávat obraným mechanismům zdravých stromů a nemohou je tak kolonizovat. Kolaps gradací je připisován především absenci spouštěcích mechanismů a chybí přesné objasnění biotických faktorů, které mohou k ukončení gradace přispět (Biedermann et al., 2019). Mortalitu kůrovců ovlivňují přirození nepřátelé, ať už se jedná o množství predátorů v podobě dravých brouků (Cleridae) nebo much (Dolichopodidae) či parazitické vosičky (Pteromelidae, Braconidae). V neposlední řadě můžeme uvést také patogenní organismy. Všechny tyto biotické faktory mohou zapříčinit kolísání populace kůrovců. Nejčastěji nalezenými patogeny u lýkožrouta smrkového, lýkožrouta severského a dalších druhů kůrovců je z prvoků *Gregarina typographi* (Fuchs, 1915) a mikrosporidie *Chytridiopsis typographi* (Weiser, 1954). Vzhledem k přenosu patogenů s potravou je často jejich hladina nižší v lesích s funkčním managementem, díky včasnému odstraňování nalétnutých kmenů (Holuša et al., 2009; Wegensteiner and Weiser, 2004; Wermelinger, 2004).

Ve střední Evropě se lesní hospodáři zabývají managementem kůrovcových disturbancí nejčastěji v malém měřítku, tedy na úrovni od jednotlivých stromů a porostů, zatímco fungování disturbancí na úrovni krajiny není dostatečně zohledněno. Avšak tento přístup může vést ke zkreslenému vnímání účinnosti a nízké efektivitě opatření managementu. K tomu, aby byla obrana účinná, je důležité, aby rizika šíření kůrovců a použitá opatření byla používána nejen na úrovni porostů, ale také v kontextu krajiny, kde bude klíčovým prvkem zaměření na propojení mezi populacemi kůrovců a jejich hostitelů (Seidl et al., 2016).

Populační dynamika kůrovců je ovlivňována množstvím faktorů ať už biotických, abiotických nebo antropogenními zásahy, například v podobě managementu. Velkou část vlivů na vznik a šíření gradací již z předešlých výzkumů a pozorování známe, i když některé jejich vlastnosti a interakce jsou stále předmětem studií. Mechanismy, které vedou k ukončování gradací však dostatečně objasněné nejsou (Biedermann et al., 2019; Sambaraju et al., 2012). I přesto, že existuje několik konceptů fungování kolapsů gradací, problematiku je třeba dále rozvíjet (Marini et al., 2013; Stadelmann et al., 2013). Kvantitativním studiím vlivu managementu na potlačování gradací se věnuje velmi malé množství studií. Výsledky jsou navíc často uváděny v rámci minulého chladnějšího klimatu a efektivita jejich využití za podmínek změny klimatu je problematická (Hlásny et al., 2019). Pro lepší pochopení mechanismů gradací bude zapotřebí výzkumů většího i menšího rozsahu k osvětlení vztahů mezi jednotlivými proměnnými, aby na základě těchto empirických vědomostí mohly být gradace ošetřeny správným managementem (Biedermann et al., 2019).

3.2 Přemnožení kůrovců a klimatická změna

Lesy jsou zásadně ovlivňovány změnou klimatu, která se projevuje kombinací oteplování, změnou režimu srážek, výskytem extrémních jevů a měnícím se režimem disturbancí (Jandl et al., 2019; Keenan, 2015; Krumm et al., 2020; Lindner et al., 2010; Marini et al., 2012). Mezi přímé dopady klimatické změny na lesní ekosystémy můžeme řadit například prodloužení vegetační sezóny nebo vliv vyšší koncentrace oxidu uhličitého na fyziologické procesy, které působí pozitivně (Weslien et al., 2009). Negativním vlivem pak mohou být nižší srážky a vyšší teplota, vedoucí k distresu z nedostatku vodních zdrojů (Zang et al., 2014). Významným nepřímým dopadem klimatické změny je vliv na změnu chování škůdců a patogenů, jejich šíření a populační dynamiku, které ovlivní lesní ekosystém (Jönsson et al., 2007; Økland et al., 2015).

Z hlediska vlivu změny klimatu přímo na populační dynamiku kůrovců můžeme dopad rozdělit na dva typy. Přímý dopad se projevuje na procesech vývoje, které jsou silně závislé na teplotě, tedy například aktivita rojení, rychlost vývoje nebo mortalita v zimním období. Nepřímo je populace zasažena dostupností stromů vhodných k vývoji (Jönsson et al., 2007). V současnosti se musíme potýkat s kůrovcovými disturbancemi extrémních měřítek, které jsou způsobeny kombinací uvedených podmínek (Seidl et al., 2011a).

S klimatickou změnou související změny teplot a posun teplotních limitů vede k rozšiřování teritorií kůrovců (Jönsson et al., 2009). Vzhledem k citlivým reakcím kůrovců na teploty, se zvyšuje závažnost průběhu a dopadů kůrovcových disturbancí v přirozených areálech výskytu, ale také probíhá šíření do nových oblastí. V těch může docházet k nedostatku potravních zdrojů, což je příčinou invaze kůrovce do nepůvodních oblastí, které jsou často díky oslabení hostitelských dřevin změnou podmínek ještě zranitelnější (Cudmore et al., 2010). Globální změna přináší také zesilování interakce mezi kůrovci a větrem. Vazby mezi změnou teploty a maximální rychlostí větru silně ovlivňují dynamiku kůrovcové disturbance (Seidl and Rammer, 2017). Změna podmínek prostředí silně ovlivňuje předpoklady obranyschopnosti stromů. Již nyní se řada zemí potýká s dopady sucha a v budoucnu se očekává, že extrémně suchá období budou častější a budou trvat déle. Nedostatkem vláhy oslabené dřeviny tak poskytnou vhodný hostitelský materiál (King and Karoly, 2017; Matthews et al., 2018). Trend zvyšování výskytu velkých kůrovcových gradací s ohledem na jejich vývoj poslední desítky let bude díky těmto podmínkám pokračovat (Seidl et al., 2014b; Senf et al., 2018).

Na druhou stranu klimatická změna může mít na šíření kůrovců i negativní efekt. Pokud jejím prostřednictvím dojde k upřednostňování listnatých dřevin snášejících vyšší teploty na úkor stromů vhodných pro kůrovce, vznikne tak deficit hostitelského materiálu (Thom et al., 2017a; Thorn et al., 2017a). S cílem snížit zranitelnost porostů vůči disturbancím a diversifikovat reakce porostů na měnící se environmentální podmínky se zvýšily snahy o obnovu přirozeného dřevinného složení (Hlásny et al., 2017; Lindner et al., 2010). Lesní plánování by v rámci globálních změn mělo uvažovat v širším kontextu a vzít v úvahu kromě potřeby zmírnit kůrovcové gradace i další požadavky lesního ekosystému, jako je například zvýšení biodiversity v obhospodařovaných porostech (Angelstam et al., 2018), změna rychlosti růstu stromů (Yousefpour et al., 2019), zmírnění změny klimatu zvýšením zásob uhlíku

(Ekholm, 2016) nebo změny prostředí a jejich dopad na společenské požadavky (Seidl and Lexer, 2013).

Pro úspěšný rozvoj velkých kůrovcových gradací jsou zapotřebí vhodné podmínky prostředí. K tomu může vést několik faktorů, mezi které se například řadí určitý počet následujících let s počasím, které umožní přežití a růst kůrovcové populace nebo dostatek hostitelských dřevin vhodných ke kolonizaci. Vhodnost hostitelských stromů je ve velké míře ovlivněna druhovou skladbou porostu a jeho věkovou strukturou, které jsou dominantními faktory ovlivňujícími závažnost kůrovcových gradací (Fettig and Hilszczański, 2015). Tyto zásadní faktory mají vzhledem k posunu teplot i množství srážek, způsobených klimatickou změnou, klíčovou roli v přežívání a šíření kůrovců. Prioritou výzkumu je tak hledat vhodné způsoby managementu k jejich omezení. Je nutné držet se předpokladu, že se lesní ekosystémy za pomoci managementu budou muset nadále vyrovnávat s podmínkami, které jim tato globální environmentální změna přináší (Bentz et al., 2010; Sambaraju et al., 2012).

3.3 Management přemnožení kůrovců

Management kůrovcových disturbancí může být rozdělen do dvou hlavních směrů. Přímé metody kontroly obsahují krátkodobé taktiky managementu, které se zaměřují ve větší míře na aktuální populace kůrovců a jejich kontrolu. Naopak nepřímé metody se zabývají možnostmi, jak přemnožením předcházet a snížit pravděpodobnost vzniku kůrovcových gradací a jejich závažnost (Fettig and Hilszczański, 2015).

Mezi jeden z hlavních nástrojů přímých metod managementu patří těžba nalétnutých stromů a materiálu vhodného pro kolonizaci kůrovci. Zde se v anglické literatuře (a tím pádem i v článcích, které tvoří jádro této práce) lze setkat se dvěma termíny, a to nahodilou těžbou (*salvage logging*) a sanitární těžbou (*sanitary logging*), které jsou často terminologicky zaměňovány, přestože se ve smyslu některých autorů liší. Na základě rozboru literatury jsou tyto termíny pro účely psaní této práce rozlišeny, a proto je v následujících řádcích jejich použitá terminologie stručně přiblížena.

Salvage logging se zaměřuje na odstraňování stromů zasažených nejčastěji větrnou disturbancí. Tyto zásahy jsou však dělány především s ohledem na zachránění alespoň části ekonomické hodnoty dřeva, která by jinak byla ztracena (Beghin et al., 2010; Stadelmann et al., 2013). Tento druh těžby se stal klíčovým nástrojem pokalamitního managementu lesa. V hospodářských lesích je provádění této těžby za účelem zabránění ztráty zisku zaviněné degradací dřeva a jeho prodejem za nižší ceny více jak oprávněné. Avšak v některých případech, jako je tomu dnes ve střední Evropě, je provádění této těžby často nákladnější, než je hodnota získaného dřeva. Tento jev je způsoben zahlceností trhu a nízkými prodejními cenami (Molinas-Gonzáles et al., 2017; Müller et al., 2018). Tuto metodu je třeba cílit na stanoviště, která mají vyšší riziko vypuknutí kůrovcového ohniska, avšak je třeba zvážit efektivitu jejich provedení (Eriksson et al., 2005).

Sanitary logging se zaměřuje na vyhledání a odstranění jednotlivých nemocných nebo hmyzem napadených jedinců z porostu za účelem zamezení jejich šíření mezi stromy okolními. Účelem sanitární těžby je především redukce populace kůrovců za podmínek, kdy se dá efektivně provádět vyhledávání jednotlivých kůrovcových stromů. Nejedná se tedy o tak intenzivní zásah jako salvage logging (Hlásny et al., 2019). Wermelinger (2004) uvádí tři základní pravidla vedoucí k efektivitě sanitární těžby: I. vyhledání a pokácení stromů musí proběhnout před vylétnutím dospělců, II. kmeny musí být odstraněny z lesa a jeho okolí případně asanovány na skládkách a III. pokud jsou v kůře již kukly nebo žlutí brouci je třeba kůru štěpkovat, či lépe spálit. Použití nahodilé nebo sanitární těžby vyžaduje důkladnou úvahu o ekonomičnosti těžby a jejích vedlejších dopadech ve srovnání s obvyklými těžebními režimy (Dobor et al., 2020a; Hlásny et al., 2019).

Další z přímých metod kontroly populací kůrovců je využívání feromonových lapačů, které dříve byly hojně využívány k odchytu kůrovců (Galko et al., 2016; Holuša et al., 2017). Tato metoda byla však primárně vyvinuta pouze pro monitoring a v současném stavu lesa ovlivněného změnou klimatu od metody většina států upouští a využívají ji pouze jako doplňkovou k jejímu původnímu účelu monitoringu a ochraně žijících stromů (Bentz and Jönsson, 2015). Účinnějším řešením k odchytu části populace kůrovců u disturbancí menšího rozsahu se tak jeví pokládání lapáků nebo stojící lapáky s feromonovou návnadou, či trojnožky. Zde je však stěžejní dodržovat pravidlo, že lapáky, které nejsou ošetřeny insekticidem, musí být sledovány a vzhledem ke stadiu vývoje kůrovce zavčas odstraněny z porostu (Holuša et al., 2017). Tak tomu být nemusí v případě využití insekticidních přípravků, které ať už v podobě kontaktních insekticidních postřiků nebo insekticidních sítí mohou mít až 100% účinnost při správné aplikaci (Zahradníková and Zahradník, 2015). Rychlým a účinným zajištěním skládek kůrovcového dřeva může být metoda fumigace. Jedná se o aplikaci insekticidu v plynném skupenství na dřevo (celou skládku) pod plachtou. V tomto případě byla nedávno vyvinuta substance EDN (etandinitril), která je schopna po určité době degradovat a neovlivní tak prostředí skládky (Stejskal et al., 2017). Využití insekticidů v boji proti kůrovci je stále kontroverzní téma. V případě jejich aplikace je nutné důkladně posoudit dopad jejich využití na necílové druhy hmyzu a tím pádem na biodiversitu stanoviště, jejich rozložitelnost a celkový vliv na prostředí (Hurling and Stetter, 2012).

Na úrovni endemických populací může být vhodnou doplňující technikou implementace predátorů, parazitoidů a patogenů jako součást biologického boje. Asi nejlepší výsledky byly zaznamenány při použití entomopatogenní houby *Beauveria bassiana* ((Bals.) Vuill., 1912). V laboratorních podmínkách její účinky dosahovaly 70–100 % mortality infikovaných jedinců. I přes její velký potenciál se využití v terénních podmínkách potýká s jistými obtížemi a je třeba vyvinout praktické metody k její aplikaci a rozšíření mezi škůdce z řad kůrovců. Její infekční hladina v podmínkách mimo laboratoř se pohybuje pouze kolem 30 % (Grodzki and Kosibowicz, 2015; Kreutz et al., 2004). Antagonisté mají na kůrovcové gradace pouze nepatrný vliv ve srovnání s faktorem odolnosti stromů. Efektivní využití jejich vlivu na kůrovcové populace dosud není přesně známo a je stále otázkou výzkumu (Galko and Pavlík, 2009; Holuša and Lukášová, 2017; Wermelinger et al., 2013).

Nepřímé metody managementu se snaží předcházet vzniku vhodných podmínek pro disturbance. Jedním z nástrojů je změna dřevinné skladby porostu. Porosty, které jsou druhově diversifikované, mají zvýšenou rezistenci vůči herbivorům (Guyot et al., 2016). Diverzifikovaný porost vykazuje silnější resilienční mechanismy. Díky změně druhové skladby jsou hostitelské stromy po porostu roztroušené a pro škůdce je obtížnější je vyhledat vzhledem k diversifikaci semiochemikálií (Seidl et al., 2014a; Zhang and Schlyter, 2003). V porostech ohrožených disturbancí je třeba vysazovat méně zranitelné a k poškození náchylné druhy, které jsou na stanovišti původní nebo jejich adaptace na podmínky neoslabí jejich obranné mechanismy (Jandl et al., 2019).

Vhodným nástrojem pro snižování rizika poškození porostů větrem a kůrovcem se jeví doba obmýtí. Jedná se o časový úsek, který uběhne mezi dvěma mýtními těžbami (Roberge et al., 2016). Délka této doby je ve velké většině hospodářských lesů střední Evropy řízena hlavně k maximalizaci produkce a ekonomických ukazatelů. V podmínkách změny klimatu je však třeba změnit uvažování a snažit se dosáhnout rovnováhy mezi kontrolou rizika disturbancí, ovlivněním množství uhlíku v lese, biodiverzitou a dalšími aspekty (Angelstam et al., 2018; Ekholm, 2016; Yousefpour et al., 2019). Věk stromu souvisí s pravděpodobností výskytu větrných disturbancí, protože postavení těžiště u vyšších stromů s větší korunou a častější výskyt poškození kmene u starších jedinců vede k většímu riziku poškození větrem. Vzhledem k preferencím středoevropského nejzávažnějšího biotického škůdce *I. typographus* v kolonizaci starších a vzrostlejších hostitelských stromů, lze předpokládat omezení rizika náletu snížením věkové struktury porostů smrku (Jactel et al., 2009). Ve smrkových porostech velké části Evropy doba obmýtí přesahuje 100 let a jsou tak vystaveny většímu riziku nejen větrné, ale právě také kůrovcové disturbance (Lindner et al., 2000). Zkrácení doby obmýtí a tedy omezení výskytu vhodných hostitelských porostů by tak mohlo vést ke snížení pravděpodobnosti výskytu ničivých kůrovcových disturbancí (Gardiner and Quine, 2000; Hlásny et al., 2017; Jactel et al., 2009). V rizikových oblastech by zaměření managementu a lesnického plánování mělo být cíleno na heterogenitu porostů. Porosty diverzifikované ve věkové struktuře, velikosti a druhovém složení mají menší riziko propuknutí kůrovcového ohniska nebo zásahu větrnou disturbancí a při zasažení disturbancí nejsou poškozeny porosty v tak velkém měřítku jako ve stejnorodých porostech (Fettig et al., 2007).

Důležitým nástrojem nepřímého managementu populací kůrovců (resp. obecně rizik) je probírka, která může ve svém důsledku omezit množství materiálu vhodného pro nálet kůrovců. (Fettig and Hilszczański, 2015). Častější probírky mohou omezit projevy sucha (Sohn et al., 2016), zvýšit diverzitu porostu, která omezuje možnosti šíření kůrovců (Honkaniemi et al., 2020), či zvýšit strukturální rozmanitost a obnovu vedoucí k snadnější regeneraci porostu po disturbanci (Churchill et al., 2013). Probírka však vede především ke snížení konkurence stromů o zdroje (např. světlo, voda, živiny), a tím je zvýšena obranyschopnost jedinců, kteří zůstanou v porostu (Oliver and Larson, 1996).

Využití nástrojů přímé kontroly bývá většinou nákladné a proto je často limitováno dostupností zdrojů, tržními a logistickými podmínkami či otázkami environmentálního vlivu (Fettig and Hilszczański, 2015). Tyto metody jsou obvykle preferovány před nepřímými postupy. Řeší problematiku kůrovců v aktuálním čase a snadněji lze pozorovat jejich účinnost na rozdíl od nepřímých nástrojů, jejichž dopad se projevuje v dlouhodobějším hledisku (McFarlane et al., 2006). Opatření nepřímého managementu mají preventivní charakter. Jejich cílem je snížit pravděpodobnost a závažnost poškození porostu kůrovci. Takovými metodami je třeba vést porosty k větší resilienci lesa, tedy schopnosti lesa odolat náporu disturbancí a rychle se po něm znovu obnovit. Nepřímé metody se zaměřují na složení porostu a jeho citlivost k budoucímu poškození (Fettig and Hilszczański, 2015). Kůrovcové disturbance patří mezi procesy lesního ekosystému velmi citlivě reagující na klimatickou změnu. Pro lesní hospodáře je management disturbancí klíčovou výzvou. Studie ukazují, že za podmínek, které se do budoucna očekávají, se některá z tradičně využívaných opatření mohou stát neúčinnými (Dobor et al., 2020a, 2019; Zimová et al., 2020). Vyhodnocení opatření managementu disturbancí by se tak měla stát prioritou výzkumu (Morris et al., 2017).

3.4 Vliv gradací kůrovce a jejich managementu na lesní ekosystémy

Každá disturbance mění celkovou strukturu lesa. Snižuje zásobu rostoucího dříví a v následujících letech také primární produktivitu krajiny. Zároveň však po disturbanci může nastoupit proces regenerace a opětovná sukcese (Zeppenfeld et al., 2015). Následující 3 kapitoly práce se věnují problematice vlivu kůrovců a jejich managementu na vybrané aspekty fungování lesního ekosystému. Kapitoly jsou strukturovány na podkapitoly dle studie Hlásny et al. (2019).

3.4.1 Vliv gradací kůrovců a jejich managementu na cyklus uhlíku

Přemnožení kůrovců má značný vliv na biochemické cykly, které v lesním ekosystému probíhají. Lesy zmírňují změnu klimatu tím, že ukládají velké množství uhlíku. Uhlík se v podobě CO_2 vyskytuje v atmosféře, kde hraje zásadní roli v probíhající změně klimatu (Chapin et al., 2006). Stromy je z atmosféry asimilován a procesem fotosyntézy přetvořen na zásoby uhlohydrátů, které jsou využívány jako zdroj energie pro růst rostlin. Celkové množství asimilovaného CO_2 fotosyntézou označujeme jako hrubou primární produkci (GPP). V důsledku nákladů na růst a zachování jednotlivých částí stromu dochází k uvolňování CO_2 z vegetace zpět do atmosféry. Jedná se o proces autotrofní respirace a jejím odečtením od GPP získáme čistou primární produkci (NPP). Čistá primární produkce se skládá ze složek produkce nadzemní (např. nadzemní části rostlin, mechy, řasy) a podzemní (např. kořeny rostlin) (Gower, 2003; Kirschbaum et al., 2001). Do koloběhu uhlíku však zasahuje také proces dekompozice, který způsobuje respiraci půdy (heterotrofní respirace). Po odečtení heterotrofní respirace od čisté primární produkce získáme hodnotu čisté produkce ekosystému (NEP). Čistá produkce ekosystému je tedy rozdíl mezi množstvím uhlíku fixovaným procesem fotosyntézy v lesním ekosystému a jeho celkovou respirací (Gower, 2003; Chapin et al., 2006). NEP je v současnosti silně ovlivněna změnou klimatu a disturbancemi. Při zásahu větrné a následně kůrovcové kalamity se uhlíková zásoba v podobě živého uhlíku snižuje se zvyšující se mortalitou stromů, ale zároveň se navyšuje jeho zásoba uložená v mrtvém dřevu. Pouze tedy s předpokladem, že určité množství uhlíku se v budoucnu bude uvolňovat z rozkládajících se stromů a tím opět vracet do koloběhu. Bez zásahu managementu je v porostu po disturbanci tedy uhlík pouze přesunut z živé biomasy do mrtvého dřeva (Bradford et al., 2008; Lindner et al., 2010). Pokud však stromy nejsou ponechány volně v lese, ale jsou odvezeny z důvodu zamezení šíření kůrovců nebo z ekonomických důvodů, dochází tak ke ztrátě uhlíku z lesa (Kurz et al., 2008). Uhlík z ekosystému ubývá také ztrátou listové plochy (Peters et al., 2013) a zvýšenou ztrátou uhlíku z půdy (Mayer et al., 2014). Častější disturbance navíc uvolňováním uhlíku do atmosféry přispívají k oteplování klimatu a tím dalšímu negativnímu ovlivnění v boji s disturbancemi (Kurz et al., 2008). Ztráta na zásobách uhlíku se vždy musí po disturbanci opět po určité době obnovit. Simulace v lesním porostu středních horských poloh střední Evropy ukazují, že aby se zásoby uhlíku po větrné a kůrovcové disturbanci opět obnovily, může to trvat desítky let. Vysoké teploty a suché podmínky změny klimatu tuto obnovu ještě prodlouží (více Dobor et al., 2018).

3.4.2 Vliv gradací kůrovců a jejich managementu na biodiverzitu

Vliv kůrovcových disturbancí na biodiverzitu je závislý na využití managementu. Například zanechávání ležící mrtvé dřevní hmoty v porostu a zároveň větší přístup světla do prostoru tvoří vhodné prostředí pro řadu lesních druhů. Určití jedinci patří dokonce do seznamu chráněných druhů rostlin a živočichů (Beudert et al., 2015). V národním parku Bavorský les, který byl během posledních 25 let silně zasažen kůrovcovými gradacemi byl zjištěný stav početnosti rostlin a živočichů dokonce srovnatelný se starověkými lesy (Hilmers et al., 2018). Působení disturbancí je však specifické pro každý druh dle jeho životní strategie a požadovaného habitatu, kdy na některé druhy může působit pozitivním a na jiné negativním efektem (Thorn et al., 2017b). Důležité je také si uvědomit, že pozitivní vliv kůrovcových disturbancí na biodiverzitu mnoha druhů je silně omezen, pokud je po disturbanci v porostech prováděn management s odstraňováním dřevní hmoty z lesa (salvage logging). Jako příklad lze uvést působení odstraňování dřevní hmoty po kalamitách, které má za následek snižování množství druhů saproxylických brouků na stanovišti, kteří jsou vázáni na výskyt mrtvého dřeva. Na druhou stranu má však toto odstranění stromů pozitivní vliv na biodiverzitu druhů spojených s otevřeným stanovištěm jako jsou například *Carabidae* (Thorn et al., 2017a).

3.4.3 Sociálně-ekonomické dopady gradací kůrovců a jejich managementu

Fungující lesní ekosystémy v mnoha ohledech pozitivně ovlivňují člověka. Analýza účinků disturbancí na ekosystémové služby ukázala, že všechny kategorie těchto služeb (zajišťovací, regulační, kulturní a podpůrné služby) jsou jejich dopadem ovlivněny převážně negativně (Thom and Seidl, 2016). Gradace mohou ve velkém měřítku ovlivnit trh a potažmo regionální ekonomiky prostřednictvím řady dopadů. Jedním z nich je negativní dopad na trh se dřevem v podobě nadměrného množství kůrovcového dřeva v nabídce, díky čemuž nastává pokles cen. Zásahem do ekonomiky může být také pokles turismu s ohledem na sníženou vizuální kvalitu lesa, či omezení pohybu po porostech. Krátkodobě může být trh práce ovlivněn i pozitivně, vzhledem ke zvýšeným požadavkům na pracovníky v lesnictví. Většina těchto dopadů je způsobena synchronizovaným prováděním managementu k odstranění rizikového materiálu na velkých plochách (Grégoire et al., 2015; Hlásny et al., 2019; Morris et al., 2017). Z dlouhodobého hlediska lze však očekávat, že během regenerace porostů po disturbancích budou omezeny zdroje dřevní hmoty. Tento proces povede ke snížení exportu a nynějších zásob na skládkách dřeva, což povede k postupnému zvyšování cen dřevní hmoty na trhu (Bogdanski et al., 2011).

Zároveň s ekonomickými dopady mají disturbance i různé sociální dopady. Gradace kůrovců vedou k rozsáhlým změnám lesní krajiny. Například padající stromy souvisejí často s omezeným či zakázaným přístupem do lesa, který je veřejností silně negativně vnímán. Navíc zpracováním disturbancí zasaženého porostu pro návštěvníky ztrácí na kvalitě estetická hodnota lesa a vnímání prostředí jako vhodného pro odpočinek. Tato ztráta estetické kvality lesa, omezený přístup nebo zrušení lesních stezek a konflikty ve využívání půdy mají těžko zhodnotitelný negativní dopad na kvalitu života (Arnberger et al., 2018; Kooistra and Hall, 2014). Návštěvníci lesních porostů tak získávají negativní zkušenost, a vizuální ráz porostu zasaženého disturbancí v nich vyvolává pocity smutku či obav (Qin et al., 2015). Reakce lidí na problematiku disturbancí a jejich managementu závisí na přístupu, jakým jim je problematika přiblížena, přičemž neúplné či nesprávné informace vedou často k sociálním konfliktům. Tyto sociální dopady mohou často vést až ke konfliktům v politické sféře (Müller, 2011). Kůrovcové disturbance tak mají vliv i na humanitní úrovni a způsobují dopady na sociální sféru (více Kapitola 5.6). Přičemž vnímaní dopadů závisí často na adaptabilitě, sociální zranitelnosti, tradicích, ekonomickém zázemí komunity a povědomí o problematice u jednotlivých případů výskytu disturbance (Qin et al., 2015). Znalost sociálních dopadů kůrovcových disturbancí a jejich managementu je velmi nedostatečná a této problematice je v budoucnu třeba věnovat více prostoru ve výzkumu (Hlásny et al., 2019).

3.5 Využití modelů pro hodnocení dynamiky přírodních disturbancí

K hodnocení komplexních dopadů disturbančních událostí se používají různé kvantitativní modely. Definičně je model zjednodušením reality a za pomoci přesného a záměrného zjednodušení se dá o fungování reálných systémů zjistit mnoho podrobností (Seidl, 2017). K modelování rozložení porostů, druhového složení, dynamiky společenstev a lesního ekosystému obecně byly vyvinuty modely s různými přístupy. Modely se pohybují od nejjednodušších teoretických modelů (Hubbell, 2001), přes modely růstu stromů a vývoje na úrovni stanoviště či krajiny (Shifley et al., 2017), až po modely simulující vývoj globální vegetace (Prentice et al., 2007).

I přesto, že za posledních 20 let se počet modelů výrazně zvýšil, převládají stále statistické koncepty nad mechanistickými (procesně orientovanými) koncepty pro explanatorní a prediktivní aplikace. Zrovna tyto koncepty jsou však rozhodujícím nástrojem pro další pochopení managementu lesních ekosystémů za působení disturbancí v rámci změn klimatu. Aktuálními výzvami v modelování disturbancí lesa jsou: a) překonat zbývající limity porozumění procesů probíhajících v lese, b) podporovat mechanistické koncepty v modelování disturbancí, c) integrovat disturbanční procesy v modelech dynamiky ekosystému určených pro podporu rozhodování v oblasti lesního managementu a d) zachytit složitost disturbančních procesů v podrobnostech jaké obnáší na všech organizačních úrovních lesa. Dosavadní modely zobrazovaly disturbance spíše jednoduše jako celek (Seidl et al., 2011a).

Modely byly často užívány jako primární nástroj k výzkumu vztahů mezi disturbancemi. Teoretické modely mohou pomoci k pochopení disturbančních vztahů z pohledu populační dynamiky (Jönsson et al., 2011). Oproti tomu simulační modely mohou být využity pro zobrazení interakcí ekosystému skrze zpětné vazby působení na vegetační strukturu a širší časové horizonty (Temperli et al., 2013).

Nová data, která přináší výzkum, jsou stále složitější, mechanické hypotézy jsou omezeně dostupné a dat je často nedostatek. Empirické a procesně orientované modely se v lesnickém managementu vyvinuly proto, aby vyřešily různé otázky a dokázaly na základě řešení navrhovat nové možnosti v lesním managementu. Empirické modely se snaží popsat statistické vztahy mezi daty s omezeným ohledem na vnitřní strukturu předmětů, pravidla nebo chování (Seidl et al., 2011a). Na druhou stranu procesně orientované modely popisují data primárně s použitím klíčových mechanismů nebo procesů, které vnitřní strukturu, pravidla a chování předmětů zkoumání determinují (Adams et al., 2013). Navíc mechanismy v procesních modelech jsou natolik obecné, že mohou poskytnout základ pro další předměty zkoumání, zatímco empirické modely zůstávají většinou využitelné pouze pro předmět, pro který byly sestaveny, tím, že se neváží na žádný specifický mechanismus. Na tomto základě se tedy procesní modely považují za výhodnější pro využití v předpovídání dynamiky lesa ať už je model na základě jednotlivého stromu, stanoviště nebo komplexně celé krajiny (Korzukhin et al., 1996).

3.5.1 Modelování dynamiky a dopadů přemnožení *Ips typographus*

Modelování hmyzích disturbancí je věnováno několik typů modelů. K základní predikci pravděpodobností jsou běžně využívány jednoduché pravděpodobnostní modely s využitím logistických regresních modelů či neuronových sítí. Takovéto modely simulují například indikátory určující stanoviště a strom a jsou nejčastěji tvořeny na základě klimatických, půdních a porostních proměnných (Ogris and Jurc, 2010). Důležitým konceptem jednoduchých pravděpodobnostních modelů je fyziologické modelování, které je zaměřeno na vitalitu hostitele a jeho vystavení stresu, tudíž i náchylnost k poškození škůdcem. Fyziologické modelování propojuje fyziologii hostitele s problematikou proměn klimatu. Toto modelování samo o sobě však nezohledňuje interakce mezi hostitelem a škůdcem (Seidl et al., 2011a). Přechodem od jednoduchých modelů k procesně orientovaným jsou fenologické modely, simulující životní cyklus hmyzu. Tyto modely zohledňují požadavky na teplotu specifické pro daný druh a jeho životní stadium, a tak reprezentují vliv klimatu na vývoj hmyzu (Jönsson et al., 2009, 2007; Wermelinger and Seifert, 1999). Potenciál výskytu kůrovců vyžaduje identifikaci klíčových proměnných, které regulují vývoj škůdce, jako například zimní mortalita, dostatek vhodných hostitelských stromů se sníženou obranyschopností, vhodné povětrnostní podmínky k šíření i pro možný vznik větrné disturbance (Fettig et al., 2007; Régnière and Bentz, 2007). Procesně orientované modely slouží k simulaci proměnných a jejich vzájemných vztahů, jako je například vztah vývoje škůdce na množství zdrojů v krajině. Tyto modely zohledňují základní vztahy mezi proměnnými až po komplikované interakce v lesním ekosystému. Příkladem komplexního procesně orientovaného modelu je iLand (Seidl et al., 2012a), který byl využit v této disertační práci.

Pro hodnocení aspektů vývoje lýkožrouta smrkového, jeho populační dynamiky a komplexních prostorových a časových interakcí v lesním ekosystému slouží množství modelů. Jako ukázku diverzity těchto přístupů se níže práce zmiňuje o několika vybraných modelech dané problematiky.

Model Phenips je fenologický model k hodnocení náletu lýkožrouta smrkového. Tento model simuluje potenciální sezónní vývoj tohoto kůrovce na základě klimatických podmínek (Baier et al., 2007). Využívá teploty vzduchu i teploty kůry k určení načasování a průběhu sezónní dynamiky lýkožrouta smrkového. V modelu se pracuje především se zahájením jarního rojení, počátkem náletu následujícím po jarním rojení, délkou vývoje generace ve stromě, počátkem dceřiné i sesterské generace a mírou, kdy neúplně vyvinuté generace dokončí plně vývoj (Berec et al., 2013). Phenips zvažuje účinky regionální topografie a stanovištních podmínek na teplotu vzduchu a kůry a využívá k tomu topoklimatická data. Jeho využití pak nejlépe slouží pro monitoring aktuálního stavu vývoje lýkožrouta na specifickém stanovišti nebo stromové úrovni. V regionálním měřítku simuluje maximální počet generací, kterých je třeba k posouzení dopadů možné kůrovcové gradace. Systém však nehodnotí konkrétní škody, které disturbance způsobí. Jeho parametrizace je nastavena pro horské oblasti střední Evropy, ale menšími úpravami parametrů dle nadmořské výšky zájmové oblasti může být adaptován pro aplikaci v širším geografickém rozsahu (Baier et al., 2007).

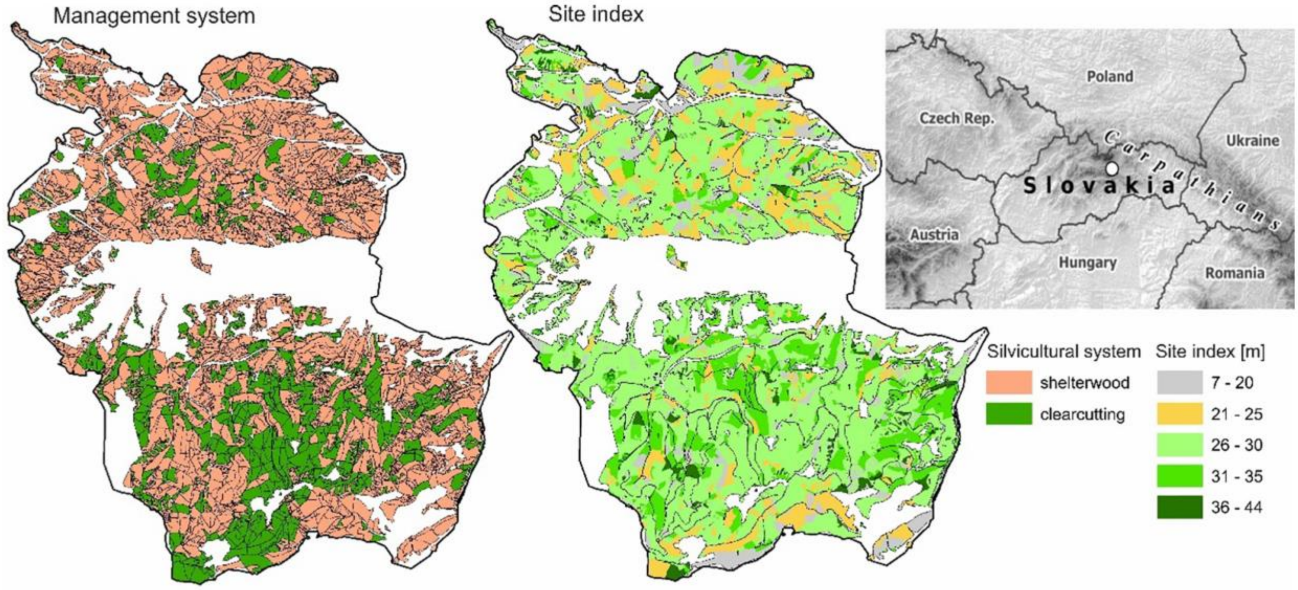
Model TANABBO, umožňuje predikci náchylnosti porostů k napadení kůrovcem na základě vybraných faktorů prostředí a jejich vlivu na hustotu populace *I. typographus* (Kissiyar et al., 2005). Tento model využívá data dálkového průzkumu země, která poskytují vizualizaci populační dynamiky škůdce. Je možné jej použít pro jakékoliv zájmové území s předpokladem, že je pro něj nutné nejprve vytvořit samostatnou geografickou databázi systému GRASS GIS (Jakuš et al., 2005). Vhodný je především pro krátkodobé prognózy. Program TANABBO je tvořen třemi skupinami modulů: Prognostická část, operační část a pomocné moduly. V pomocných modulech se nachází vegetační indexy a import údajů. Prognostická část obsahuje submoduly pro výpočty dynamiky a prognóz poškození porostu lýkožroutem smrkovým, možnost validace a testování prognostických metod a podporu v oblasti managementu lesa. Zohledněna je zde i vyšší pravděpodobnost napadení porostů po větrné kalamitě. V operační části se nachází výše zmíněný modul pro výpočet vývoje lýkožrouta Phenips, moduly teploty vzduchu a kůry, potenciální solární radiace, korekce dle meteorologických měření, index sucha, deficit vláhy a rizika sucha. Operační prognózy jsou stanovovány právě především na základě fenologického modelu Phenips, případných pozorování z monitorovacích feromonových lapačů a submodulu pro výpočet indexu sucha a kumulativního transpiračního deficitu. TANABBO je systém, který na základě identifikace ohrožených porostů přinese včasné varování před náletem škůdce (Jakuš et al., 2017).

V této práci využitý model iLand je procesně orientovaný model, který simuluje dynamiku lesního ekosystému včetně vlivu disturbancí (Seidl et al., 2012a). Simulace zohledňují především hlavní demografické procesy v lesním ekosystému, mezi které patří například růst, regenerace nebo mortalita, a procesy jako koloběh uhlíku, dusíku a vody (Mäkelä, 2003). iLand patří mezi modely simulující vývoj jednotlivých stromů. Tyto modely se mohou využívat k získání velkého rozsahu různých poznatků a mají tak v lesnictví a ekologii dlouhou tradici (Maréchaux et al., 2021). Základní mortalita stromů způsobená stresem je v modelu simulovaná na základě procesně orientovaného přístupu k vyčerpání nestrukturálních karbohydrátů (Seidl et al., 2012a). Jsou zde zastoupeny tři disturbanční činitelé (kůrovec, vítr a požáry), které jsou připojeny v samostatném modulu, který může být individuálně upraven na základě změny jeho parametrů (Seidl et al., 2012a). Více v části práce 4.2–4.4.

4 Metodika

4.1 Vymezená studijní lokalita a klimatická data

V rámci předložené disertační práce jsou uvedeny 4 případové studie modelování managementu kůrovcových gradací v podmínkách změny klimatu (Kapitola 5.1, 5.2, 5.3 a 5.4). Studijní plochou těchto prací je oblast Nízkých Tater, nacházející se ve středovýchodní části Slovenska o rozloze 16 050 ha. Dominantní dřevinou lesních porostů je smrk ztepilý se 70% zastoupením v dřevinné skladbě, přičemž jeho porost činí 75 % z celkové zalesněné plochy. Dalšími nejdůležitějšími druhy jsou například modřín opadavý, borovice lesní, jedle bělokorá a z listnatých především buk lesní. Území je spravováno holosečným způsobem v oblastech, které jsou složeny čistě ze smrku. Dominantním způsobem obnovy je však seč clonná využívaná v oblastech s porosty jedle a buku (Obr. 1). Průměrná doba obmýtí je v porostech přibližně 100 let.



Obr. 1 Management uplatňovaný na studijní lokalitě (vlevo). Smrk je obhospodařován holosečným způsobem (zelená) a ve smíšených porostech se uplatňuje clonná seč (růžová). Site index (vpravo) ukazuje průměrnou výšku porostů ve věku 100 let. V přiložené mapě je označeno umístění studované plochy.

V případových studiích byly ke spuštění simulací využity dva typy klimatických dat. Referenční klimatická data vznikla na základě údajů z meteorologické stanice Poprad – Gánovce, na jejichž podkladě vznikla řada klimatických dat náhodným řazením roků podrobněji Dobor et al. (2018). Klimatická změna byla skupinou scénářů změny klimatu řízených scénáři koncentrací skleníkových plynů (Representative Concentration Pathway – RCP) RCP 4.5 a RCP 8.5 (Kapitola 5.1, 5.2, 5.3 a 5.4)

4.2 Simulační model iLand

K simulaci složité dynamiky lesního ekosystému včetně vzájemných interakcí byl využíván model iLand (individual-based forest landscape and disturbance model), který simuluje funkční, strukturální a prostorové procesy na úrovni jednotlivých stromů a krajiny. Tento model simuluje dynamiku lesního ekosystému v podmínkách změny klimatu a vlivu disturbancí, se zvláštním zaměřením na modelování interakcí a zpětných vazeb mezi managementem, klimatem a disturbančními režimy (Seidl et al., 2012a). Tento procesně orientovaný systém funguje na základě víceúrovňového propojení ekologie krajiny, systémové ekologie a ekologie společenství (Mäkelä, 2003).

iLand pracuje na úrovni jednotlivých stromů. Umístění každého stromu na ploše spolu s jeho reakcí na kompetici poskytuje procesně orientovaný indikátor úspěšnosti jednotlivých stromů v konkurenčním boji o zdroje. Produktivita je simulovaná na základě adaptivního chování stromů na jejich prostředí. Především se jedná o efektivitu využívání světla na stanovišti (Seidl et al., 2012a).

Přirozená mortalita je v iLandu simulovaná na základě vyčerpání zásob karbohydrátů (carbon starvation). Model tak kombinuje vnitřní složku mortality, která je založena na vlastnostech a stanovištních požadavcích jednotlivých druhů dřevin (Keane et al., 2001) a složku mortality způsobenou stresem ve spojení s vyčerpáním karbohydrátů (Güneralp and Gertner, 2007). Tyto procesy jsou simulovány na úrovni každého jednotlivého stromu s přihlédnutím na adaptivní chování stromů, které je následkem jejich přizpůsobování přírodnímu prostředí (Seidl et al., 2012a). Všechny události způsobující mortalitu stromu (výjimkou je těžba) vedou ke vzniku stojícího mrtvého dřeva. Listový pokryv a biomasa jemných kořenů jsou v roce úhynu stromu přesunuty do humusové vrstvy půdy, zatímco větve a silnější kořeny jsou dále součástí ležícího mrtvého dřeva a jejich rozklad je rovnoměrně rozdělen do následujících 5 let po úhynu stromu (Seidl et al., 2012b).

4.3 Implementace disturbancí

Mortalita v důsledku disturbancí je v modelu implementována v podobě samostatných modulů. Tyto moduly pro disturbance jsou zde zpracovány pro 3 disturbanční činitele, a to kůrovce, vítr a požáry. Každý modul může být individuálně spuštěn nebo vypnut a upraven na základě změny jeho jednotlivých parametrů (Seidl et al., 2012a). S ohledem na zaměření práce zde následuje stručný popis implementace poškozování porostů větrem a kůrovcem.

4.3.1 Kůrovcový modul

Kůrovcový modul iLandu v simulaci dynamiky vztahů mezi kůrovcovou disturbancí, prostředím a klimatem zohledňuje fenologii kůrovců, jejich vývoj, prostorové šíření, kolonizaci hostitelského stromu, jeho obranné reakce a stejně tak i ovlivnění antagonisty a dalšími faktory. Modul je nastaven tak, aby zohlednil všechny řídící procesy, které kůrovcovou disturbanci ovlivňují na všech úrovních. Těmito procesy jsou především na úrovni stromu jeho zranitelnost vůči škůdci a obrana, pro stanoviště se jedná o teplotní požadavky a fenologii kůrovců. Na úrovni krajiny zohledňuje distribuci hostitelských stromů i kůrovců a v regionálním měřítku kolísání klimatických podmínek a extrémy, které mohou spustit gradaci. Parametrizace modulu vznikla na základě odborné literatury. Dle původního účelu je nastavena k implementaci na systém smrku ztepilého a lýkožrouta smrkového. Její nastavení je však natolik obecné, že po několika změnách je možné využít jej i pro jiného kůrovce (Seidl and Rammer, 2017).

Modul se skládá z parametrů, které se dají rozdělit do skupin: iniciace gradace lýkožrouta, disperze dospělců, kolonizace hostitele, přezimování a kolaps gradací.

Vzhledem k významnosti kůrovcového submodulu jsou v této práci uvedeny v následujících několika odstavcích jeho nejdůležitější součásti. Dané parametry jsou uvedeny rozdělené do skupin a jsou stručně popsány.

Parametry iniciace gradace lýkožrouta

P_{base} – Jedná se o vypočtenou roční pravděpodobnost výskytu kůrovcové disturbance. Hodnota je vypočtena na základě pozorované periody mezi jednotlivými disturbancemi. Tato perioda může být zjištěna na základě dendrochronologických údajů (Čada et al., 2013) nebo historických záznamů o výskytu disturbancí (Thom et al., 2013). Může být definována jako prostorově jednotná pravděpodobnost pro celou krajinu, ale také může být vyjádřena jako mapa, která odpovídá prostorovému rozdělení této pravděpodobnosti po území. Pravděpodobnost vzniku kůrovcových ohnisek se výrazně liší rok od roku. Nedávné studie spouštěcích mechanismů ukazují, že změny klimatu v regionálním měřítku jsou důležitým faktorem pro iniciaci gradací (Seidl et al., 2016).

r_c – modifikátor citlivosti klimatu je měřítkem relativních změn klimatických podmínek, pro které byl stanoven parametr P_{base}. V regionálním měřítku propojuje změny klimatu mezi roky a je tak uniformní pro celou krajinu. Je stanoven buď na základě klimatických vztahů během gradace, zjištěných modelováním nebo empirickými analýzami a je závislý na relativních letních srážkách předchozího roku ve vztahu k dlouhodobému průměru (Seidl et al., 2016).

$P_{windthrown}$ – pravděpodobnost nalétnutí stromů zasažených větrem kůrovci. Tento parametr je stanoven na základě empirických dat uvedených v publikaci Eriksson et al. (2005).

Parametry šíření dospělců

K_{spread} – vypočítává pravděpodobnost, že se imaga rozšíří do x metrů z původní oblasti, kde gradace začala. Jádro funkce je převzato z Fahse and Heurich (2011).

$N_{cohorts,\ main}$ – vyjadřuje míru reprodukce brouků, tedy počet kůrovcových kohort, které se rozšíří z nalétnutých pixelů za každou generaci. Empirické výzkumy udávají velmi proměnlivé hodnoty mezi 4 a 24 (Wermelinger and Seifert, 1999).

$N_{cohorts,\ sisterbroods}$ – míra reprodukce dospělců přičítaná k hlavní generaci, pokud se plně vyvine a vylétne sesterské rojení. Předpokládá se, že míra reprodukce během sesterského rojení je o polovinu nižší než u rojení hlavní generace

Kolonizace hostitelských stromů

DBH_{min} – hraniční průměr stromů ve výšce 1,3m, od kterého je strom možno považovat za potenciálního hostitele vhodného pro nálet lýkožrouta

$P_{colonize}$ – pravděpodobnost úspěšného náletu jednou kohortou vyjádřená jako funkce stress indexu, který závisí na rovnováze uhlíku (Seidl et al., 2012a).

Přezimování

M_{bg} – mortalita během přezimování. Fixní množství imag během přezimování uhyne (Jönsson et al., 2012).

M_{w} – přidaná hodnota mortality při výskytu dní s minimální teplotou nižší než -15°C (Koštál et al., 2011).

Kolaps gradací

M_{nf} – přidaná hodnota mortality vzhledem k antagonistům a snížené kondici dospělců v pozdějších stadiích gradace. Jak a proč gradace najednou skončí, ještě není zcela vysvětleno. Literatura se však víceméně shoduje v názoru, že regionální kůrovcové gradace vždy po 6 letech skončí (Seidl et al., 2016). Antagonisté jako predátorské včely, parazitické mouchy a ptáci, hrají důležitou roli ve zmírňování kůrovcových gradací (Wermelinger, 2004).

Již počáteční hodnocení integrovaného kůrovcového modulu v rámci testování krátké řady kůrovcových disturbancí ukázalo velmi vysokou spolehlivost dat vycházejících z modelu. Výsledky simulací v porovnání s daty reálně pozorovanými ve stejné lokalitě uspokojivě reprodukovaly disturbance. Přestože simulace vykazovaly jistou míru odchylky od reálných dat (nadhodnocení i podhodnocení), jejich spolehlivost se pohybovala od 80 % výše (Seidl and Rammer, 2017). V práci Sommerfeld et al. (2020) byly zevrubně testovány prostorové a časové vzorce simulovaných disturbancí, které byly následně porovnávány s nezávislými daty (Kautz et al., 2011). Kůrovcový modul opět vykazoval ve výsledcích vysokou míru spolehlivosti (Sommerfeld et al., 2020). Model iLand byl během posledních let důkladně testován a jeho podoba včetně modulů byla upravována na základě simulací pro různé typy lesů střední Evropy a západní části USA. Jeho simulace produktivity, vegetační dynamika a disturbanční vzorce tak byly úspěšně srovnávány s reálnými pozorovanými daty (Seidl et al., 2018).

4.3.2 Modul poškozování porostů větrem

Modul poškozování porostů větrem musí vzít v úvahu dynamickou strukturu stanoviště a krajinný rámec v kombinaci se silou větru jakožto vnějším činitelem. Procesní model iLand simuluje větrné disturbance na základě informací o aktuální rychlosti větru, které byly v případě této práce získány z meteorologických stanic umístěných v okolí zájmové krajiny. Zásahy větrem jsou pak definovány rychlostí (průměrná hodinová rychlost větru) a směrem vanutí. Poškození porostů pak způsobují pouze ty větrné události, které překročí určitou rychlost. Časové řady větrných podmínek lze dosadit vygenerováním z klimatických modelů nebo z empiricky zjištěné distribuce rychlostí větru, stejně tak může být determinován i den větrné události a délka jejího trvání (podrobněji Kapitola 5.3, Seidl et al., 2014b, Seidl and Rammer, 2017). Předpokládá se, že velké větrné disturbance zasáhnou především na okrajích lesního porostu (Blennow and Sallnäs, 2004). V iLandu jsou za místa potenciálně ohrožená větrem považovány pouze buňky, jejichž stromová výška dosáhne hranice 10 m vrchní výšky stromových korun (Seidl et al., 2014a). Ve výpočtech modulu je samozřejmě zvažován efekt umístění porostních okrajů, vegetace na návětrné straně a také efekt krytu sousedních stromů, případně jejich nedostatek (Hale et al., 2012). Zásahem větru vznikají zlomy, či vývraty, přičemž kritická rychlost je pro každý druh poškození počítána zvlášť dle Gardinera et al. (2000). Tímto poškozením jsou odkryty další stromy v porostu utvářející nový okraj, který je při dalším zásahu větrem zranitelnější a je modelem zvažován v dalších výpočtech. Větrný modul je tak při zohlednění rozdílů v terénním uspořádání, zranitelnosti a struktuře vegetace funkčním a poměrně přesným nástrojem k zohledňování dopadů silného větru (Seidl et al., 2014a).

4.4 Implementace managementu do modelu iLand

Aby bylo v simulacích možno zohlednit také dynamické propojení faktorů přírodních a sociálních systémů, iLand obsahuje i nástroje pro simulaci managementu lesa. Systém simulace managementu zahrnuje všestranný přístup s širokým spektrem hospodářských zásahů. Pracuje na základě modulu umožňujícího simulovat současně několik činitelů managementu, změna managementového plánu je tak prováděna dynamicky. V rámci výsadby model umožňuje ovlivnit výšku, věk a druh vysazovaných sazenic. Ve výsadbě porostních směsí je možné upravit zastoupení jednotlivých vysazovaných druhů a tím ovlivnit cílovou dřevinnou skladbu lesa. Výchova porostu v podobě prořezávek a probírek a následná mýtní těžba jsou v modelu prováděny dynamicky dle vývoje jednotlivých stanovišť a je možné je ovlivnit několika parametry. Těžba tak může být přizpůsobena dle tloušťkových tříd stromů, množství stromů na hektar nebo objemu dřevní hmoty, které chceme vytěžit, či naopak ponechat na stanovišti. Ve studii zkracování doby obmýtí byl využit parametr věku, kdy model vybírá k těžbě jedince dosahující určitého stáří. Nahodilá těžba je v modelu aktivita uplatňovaná na plochách, které ovlivnila disturbance. Pokud je plocha modelem vyhodnocena jako zasažená, model automaticky spustí těžbu/odstraňování poškozených stromů. Na velkých plochách pak model automaticky resetuje obmýtí. V rámci předkládaných studií byla využita možnost změny intenzity provádění zásahu nahodilé těžby a také její prostorové umístění do určitých částí porostu. Tyto zásahy managementu mohly být simulovány samostatně či ve vzájemných kombinacích. Změna parametrů managementu našich studií proběhla úpravou JavaScriptového souboru, se kterým model pracuje.

4.5 Design jednotlivých studií

Čtyři studie uváděné v této práci jsou zaměřeny na simulaci zásahů managementu a jejich vlivu na disturbance kůrovců za podmínek změny klimatu. Základní nastavení modelu je pro všechny tyto studie stejné a je uvedeno v Kapitolách 5.1, 5.2, 5.3, 5.4. Podrobněji jsou zde uvedeny pouze zásadní charakteristiky jednotlivých studií, ve kterých se odlišují.

4.5.1 Zkracování doby obmýtí jako nástroj pro snižování rizika disturbancí – potenciál a omezení.

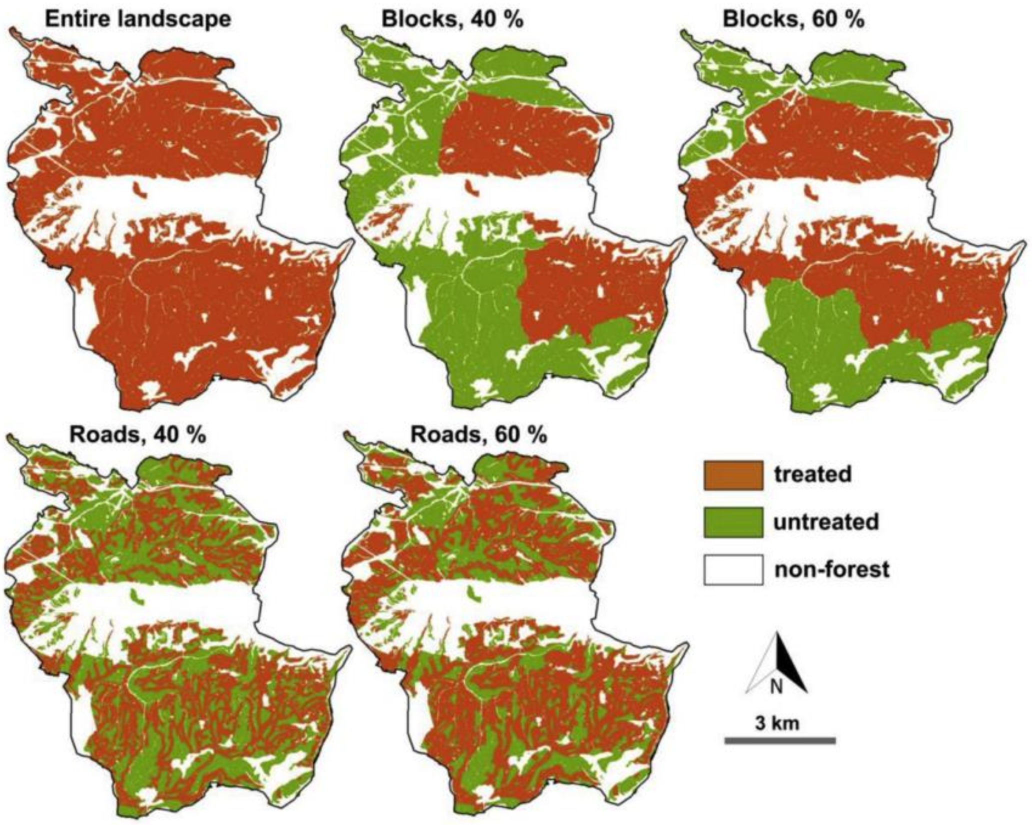
Stěžejní charakteristikou bylo zkrácení doby obmýtí, které je reálně ve studijní lokalitě upraveno lesnickou legislativou, kdy průměrná doba obmýtí smrkových stanovišť je 100 let a u listnatých stanovišť 115 let. Tyto hodnoty byly stanoveny jako výchozí a z nich byly odvozeny a simulovány 4 alternativní scénáře s relativním zkrácením doby obmýtí o 10, 20, 30 a 40 %. Nicméně hodnota doby obmýtí nesměla klesnout pod 60 let. Všechny tyto managementové scénáře byly simulovány jak v referenčním klimatu, tak v podmínkách změny klimatu. Během průběhu simulace dlouhé 200 let bylo simulováno průběžně 6 větrných událostí. Hodnoceny byly jak krátkodobé efekty v prvních 30 letech samotné simulace, tak efekty dlouhodobé ve zbylých 170 letech (Kapitola 5.1).

4.5.2 Nahodilá těžba jako efektivní nástroj ke ztlumení šíření kůrovce a zachování uhlíku v lese

Simulováno bylo sedm různých intensit provádění nahodilé těžby a to 0, 20, 40, 60, 80, 95 a 100% intenzita odstranění kůrovcového materiálu ze stanoviště. Stromy poškozené větrem či kůrovcem byly odstraněny ve stejném roce, ve kterém došlo k disturbanci a neprobíhala zde preventivní těžba živých stromů (sanitární těžba). Simulace dlouhé 200 let proběhly s pěti různými větrnými scénáři obsahujícími 5 větrných událostí s různou distribucí během let. Všechny tyto možnosti managementu a větru proběhly také ve spojení s 13 různými klimatickými scénáři (Kapitola 5.2).

4.5.3 Prostorové rozmístění nahodilé těžby ovlivňuje kůrovcové disturbance

Experimentální design této studie spočíval v simulaci třech druhů prostorového rozmístění nahodilé těžby v různých intenzitách. První rozmístění je uniformní těžba po celé ploše s různými intenzitami nahodilé těžby (viz Kapitola 5.2). Druhým typem je soustředění nahodilých těžeb do okolí lesních cest. Tento typ představuje omezené možnosti managementu disturbancí v podobě provádění opatření v dobře přístupných oblastech. Naopak posledním typem rozmístění je provádění nahodilé těžby v určitých blocích (Obr. 2). Tento přístup počítá s možností, že v některých oblastech těžba není možná například z důvodu ochrany přírody. Poslední dva zmíněné způsoby byly simulovány ve scénáři pokrytí 40 a 60 % celkové plochy tímto způsobem managementu a také o dvou různých intenzitách nahodilé těžby 60 a 95 % (Kapitola 5.3)



Obr. 2 Schéma prostorového rozmístění nahodilé těžby na lokalitě. Procenta uvádějí, kolik z celkové plochy bylo ošetřeno managementem.

4.5.4 Role managementu kůrovcových disturbancí v monokulturních a druhově rozmanitých lesích

Předkládaná studie je shrnutím a rozšířením problematiky managementu v předchozích předložených případových studiích. Simulace představovaly různé vzájemné kombinace a nastavení přístupů ke zvládnutí kůrovcových disturbancí. Součástí simulací bylo provádění nahodilé těžby, různá délka obmýtí a změna v cílovém složení dřevin na stanovišti. Studie byla tedy vyhotovena v souladu s problematikou lesnictví ve střední Evropě, a dilematem, zda zachovat velký podíl smrku kvůli zpracovatelským/ekonomickým účelům nebo vysazovat cíleně ostatní druhy dřevin ke vzniku druhově diversifikovaného porostu, který se blíží přírodnímu složení (více v Kapitola 5.4).

4.6 Design podpůrných studií

Kromě výše uvedených studií zaměřených na modelování zásahů vedoucích k optimalizaci managementu lesa je práce doplněna o dvě podpůrné studie, které svou tématikou vhodně doplňují problematiku kůrovcových disturbancí.

4.6.1 Infekční hladina mikrosporidie *Larssoniella duplicati* u invazního druhu kůrovce *Ips duplicatus*

Příspěvek o vlivu mikrosporidie na populační dynamiku kůrovce vztaženou k ohniskům jeho výskytu v původním i novém areálu vznikl na základě odběru vzorků kůrovce *Ips duplicatus* z lapačů ve 4 státech (Švédsko, Polsko, Česká republika, Rumunsko) sledujícího šíření kůrovce Evropou. Každý jedinec byl vypitván a mikroskopován pro zjištění přítomnosti mikrosporidie i dalších patogenů. Statistické analýzy sledují vztah mezi infekční hladinou mikrosporidie a dalšími proměnnými (Kapitola 5.5).

4.6.2 Vývoj kůrovcové kalamity v České republice, její spouštěcí mechanismy, dopady a vliv managementu.

Na základě několika zdrojů (Lesní ochranná služba, Český statistický úřad a Ústav hospodářské úpravy lesa) byla zkompletována a zkombinována data o škodách kůrovcem v jednotlivých okresech České republiky v období let 2003–2019. Studie se podrobněji zaměřuje na periodu 2017–2019, kdy kůrovcová gradace dosáhla nebývalé intenzity. Tato data byla zkoumána v souvislosti s prediktory klimatu a lesní struktury. Navíc bylo prozkoumáno množství volně dohledatelných materiálů reportáží a zpráv k porozumění dopadu disturbance na sociální, ekologický a ekonomický sektor (Kapitola 5.6).

5 Výsledky

Předložená disertační práce vznikla na základě 6 odborných článků, zabývajících se problematikou, která je součástí jednotlivých cílů práce. Na kapitoly výsledků obsahující jednotlivé publikace je odkazováno v předchozích kapitolách.

Problematikou managementu kůrovcových disturbancí se zabývají 4 publikace. První publikace je zaměřena na využití nástroje zkracování doby obmýtí:

Kapitola 5.1) ZIMOVÁ, S., DOBOR, L., HLÁSNY, T., RAMMER, W., SEIDL, R., 2020. Reducing rotation age to address increasing disturbances in Central Europe: Potential and limitations. Forest Ecology and Management 475. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118408

využití nástroje managementu kůrovcových gradací v podobě nahodilé těžby prováděné v různé intenzitě a různém rozložení provádění těžby ve vymezené lokalitě je popsáno v publikacích:

Kapitola 5.2) DOBOR, L., HLÁSNY, T., RAMMER, W., ZIMOVÁ, S., BARKA, I., SEIDL, R., 2019. Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? Journal of Applied Ecology 57, 67–76. https://doi.org/10.1111/1365-2664.13518

Kapitola 5.3) DOBOR, L., HLÁSNY, T., RAMMER, W., ZIMOVÁ, S., BARKA, I., SEIDL, R., 2020. Spatial configuration matters when removing windfelled trees to manage bark beetle disturbances in Central European forest landscapes. Journal of Environmental Management 254, 1–12. https://doi.org/10.1016/j.jenvman.2019.109792

využitím různých kombinací předešlých 2 nástrojů managementu a nástroje postupné změny dřevinné skladby se zabývá publikace:

Kapitola 5.4) DOBOR, L., HLÁSNY, T., ZIMOVÁ, S., 2020. Contrasting vulnerability of monospecific and species-diverse forests to wind and bark beetle disturbance: The role of management. Ecology and Evolution 10, 1–13. https://doi.org/10.1002/ece3.6854

Výše uvedené výsledky byly doplněny také následujícími podpůrnými studiemi, kde k empirickému výzkumu mechanismů, které mohou ovlivnit populační dynamiku kůrovce přispívá výstup:

Kapitola 5.5) ZIMOVÁ, S., RESNEROVÁ, K., VANICKÁ, H., HORÁK, J., TROMBIK, J., KACPRZYK, M., LINDELÖW, Å., DUDUMAN, M., HOLUŠA, J., 2019. Infection Levels of the Microsporidium *Larssoniella duplicati* in Populations of the Invasive Bark

Beetle *Ips duplicatus*: From Native to New Outbreak Areas. Forests 10, 1–10. https://doi.org/10.3390/f10020131

a shrnutím vývoje kalamity kůrovce v České Republice, její prognostikou a stručným hodnocením jejích dopadů na sociální, ekologickou a ekonomickou oblast se zabývá:

Kapitola 5.6) HLÁSNY, T., ZIMOVÁ, S., MERGANIČOVÁ, K., ŠTĚPÁNEK, P., MODLINGER, R., TURČÁNI, M., 2021. Devastating outbreak of bark neetles in the Czech Republic: Drivers, impacts, and management implications. Forest Ecology and Management 490, 1–13. https://doi.org/10.1016/j.foreco.2021.119075

5.1 Reducing rotation age to address increasing disturbances in Central Europe: Potential and limitations

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Reducing rotation age to address increasing disturbances in Central Europe: Potential and limitations

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ABSTRACT

Forest disturbance regimes are intensifying in many parts of the globe. In order to mitigate disturbance impacts a number of management responses have been proposed, yet their effectiveness in addressing changing disturbance regimes remains largely unknown. The strong positive relationship between forest age and the vulnerability to disturbances such as windthrows and bark beetle infestations suggests that a reduced rotation length can be a potent means for mitigating the impacts of natural disturbances. However, disturbance mitigation measures such as shortened rotation lengths (SRL) can also have undesired consequences on ecosystem services and biodiversity, which need to be considered in their application.

Here, we used the process-based landscape and disturbance model iLand to investigate the effects of SRL on the vulnerability of a 16,000 ha forest landscape in Central Europe to wind and bark beetle disturbances. We experimentally reduced the current rotation length (between 100 and 115 years) by up to −40% in 10% increments, and studied effects on disturbance dynamics under current and future climate conditions over a 200-year simulation period. Simultaneously, we quantified the collateral effects of SRL on forest carbon stocks and indicators of biodiversity. Shortening the rotation length by 40% decreased disturbances by 14%. This effect was strongly diminished under future climate change, reducing the mitigating effect of shortened rotation to < 6%. Collateral effects were severe in the initial decades after implementation: Reducing the rotation length by 40% caused a spike in harvested timber volume (+92%), decreased total forest carbon storage by 6% and reduced the number of large trees on the landscape by 20%. The long-term effects of SRL were less pronounced. At the same time, SRL caused an increase in tree species diversity. Shortening rotation length can reduce the impact of wind and bark beetle disturbances, but the overall efficiency of the measure is limited and decreases under climate change. Given the potential for undesired collateral effects we conclude that a reduction of the rotation length is no panacea for managing increasing disturbances, and should be applied in combination with other management measures reducing risks and fostering resilience.

1. Introduction

Forest disturbances have increased in recent decades, and there is ample evidence that this trend will continue in the future due to ongoing climate change (Seidl et al., 2014b; Senf et al., 2018). Among the forest types affected by recent pulses of mortality, Europe‘s Norway spruce forests (*Picea abies* (L.) Karst) were impacted with a particular severity (Dobor et al., 2018; Marini et al., 2017; Mezei et al., 2017). The sensitivity of these forest types to large-scale dieback is on the scientific agenda since the 1980‘s (Hlásny and Sitková, 2010; Klimo et al., 2000), yet recent observation are particularly alarming and suggest that a tipping point has been reached (Hlásny et al., 2019; Lindenmayer et al., 2016). While the initial problems identified in the 1980 largely concerned areas where the species was cultivated at the edge of or even outside of its natural range, recent pulses of mortality occurred almost across the entire distributional range of the species in Central Europe (de Groot et al., 2019; Marini et al., 2017).

These developments have promoted the adoption of new policies which mainly strived to restore the natural tree species composition (Hlásny et al., 2017; Spiecker et al., 2004), aiming to increase the response diversity to changing environmental conditions and reduce the vulnerability to disturbances (Lindner et al. 2010). While the forest policy and management communities in Central Europe have largely focused on the question of which tree species and species mixtures

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could increase the robustness of forest stands to changing climate and disturbance regimes (e.g. Bolte et al. 2009), recent research indicates that also other management options provide considerable leverage. These, for instance, include intensifying thinnings to reduce drought risk (Elkin et al., 2015; Sohn et al., 2016), improving structural diversity and revegetation strategies to facilitate post-disturbance regeneration (Churchill et al., 2013; Lafond et al., 2014), and increasing landscape-scale diversity to contain the spread of disturbances (Honkaniemi et al., 2020; Seidl et al., 2018).

Another important means to influence the structure and functioning of managed forests is the timing of harvesting operations (Brown et al., 2018; Curzon et al., 2017; Russell and Jones, 2001). A central parameter in this regard, describing the time elapsed between final fellings in even-aged forest management, is rotation length (Roberge et al., 2016). In Central Europe, rotation lengths are typically determined based on past species- and site-specific growth performance to maximize profit (Faustmann, 1849; Newman, 2002). Forest planning under global change, however, requires broader consideration, accounting, for example, for changing tree growth performance (Blennow et al., 2010; Yousefpour et al., 2019), the need to mitigate climate change via increased carbon stocks (Ekholm, 2016; Liski et al., 2011), the requirement to increase biodiversity also in managed forests (Angelstam et al., 2018; Díaz-Rodríguez et al., 2012), and the uncertainty in future environmental conditions and societal demands (Daniel et al., 2017; Seidl and Lexer, 2013; Spittlehouse and Stewart, 2003).

The risk for many disturbances changes with stand age (Gardiner and Quine, 2000; Jactel et al., 2009; Roberge et al., 2016). Disturbances are thus another important factor to consider in determining forest rotation length (Meilby et al., 2001; Price, 1989). In the Norway spruce forests of Central Europe, the most important biotic disturbance agent is the European spruce bark beetle *Ips typographus* (L.). It typically prefers trees older than 60 years that have a diameter at breast height larger than 20–25 cm (although beetles may attack and reproduce also in smaller and younger trees at high population levels). A similar positive relationship between tree age and susceptibility exists for wind disturbance (Jactel et al., 2009). Taller trees receive higher wind loading (larger crown surface area) and turning moments (higher crowns), leading to an increased risk of windthrow and stem breakage. Moreover, considering the long disturbance return intervals and the stochastic nature of wind regimes, a longer rotation increases the chance that a severe windstorm will occur during the lifetime of a tree generation in a particular area (Jactel et al., 2009). Wind disturbance furthermore often serves as trigger for bark beetle outbreaks (Marini et al., 2017), an interaction that is expected to be further amplified under climate change (Seidl and Rammer, 2017). That the rotation length in Norway spruce forests exceeds 100 years in many regions of Europe (Lindner et al., 2000) thus results in large tracts of forests prone to both wind and bark beetle disturbances. Therefore, a shortening of the rotation length is increasingly discussed as a means to address intensifying disturbance regimes (Gardiner and Quine, 2000; Hlásny et al., 2017; Jactel et al., 2009; Kuboyama and Oka, 2000).

Reducing rotation length, however, can also have negative effects on the supply of ecosystem services (e.g., timber production, carbon storage) and the objectives of nature conservation (Felton et al., 2017; Roberge et al., 2016). Reducing rotation length can, for instance, result in a temporal surplus of timber to the market and reduce the supply of logs with larger dimensions (Lindner et al., 2000). Shorter rotation may also result in a loss of habitat features that are important for biodiversity conservation (Felton et al., 2017; Lange et al., 2014; Lassauce et al., 2013) and compromise supporting (water, soil nutrients) and cultural (aesthetics, cultural heritage) ecosystem services (Roberge et al., 2016; Weslien et al., 2009). The reduction of mature stands with high structural complexity can, for instance, affect habitat availability for some red-listed species (Bernes, 2011) and reduce the amount of dead wood, which accumulates with a higher intensity in older stands (Jonsson et al., 2006). The absence of old trees and the higher frequency of harvesting interventions can also affect forest aesthetic and recreation values negatively (e.g. Curtis, 1997). Reduced forest carbon stocks due to shorter rotation may counteract efforts to mitigate climate change through carbon storage in forest ecosystems (Ekholm, 2016; Kaipainen et al., 2004). Recent research also indicates that the maintenance of older forests on the landscape can help to sustain biodiversity and ecosystem services under climate change (Thom et al., 2019).

Here, we assessed how a reduced rotation length affects the future susceptibility of forests to wind and bark beetle disturbances. We subsequently evaluated a range of collateral effects of reduced rotation lengths, assessing their impact on indicators of forest carbon storage and biodiversity. We hypothesized that a reduced rotation length can buffer the expected increase in forest disturbances in the forests of Central Europe (Björkman et al., 2015; Jactel et al., 2009). However, we further expected that positive effects on disturbance risk are countered by negative effects of reduced rotation on indicators of forest carbon and biodiversity (Liski et al. 2011, Lassauce et al. 2013, Lundmark et al. 2018).

2. Methods and materials

2.1. Simulation model

To address the complex interdependencies between disturbance, rotation, and indicators of ecosystem services and biodiversity, we here used the forest landscape and disturbance model iLand (Seidl et al., 2012a). iLand is a process-based ecosystem model that simulates forest landscape dynamics within a hierarchical multi-scale framework (Mäkelä, 2003), i.e. the model treats different processes at different spatial and temporal scales. The main entity in the model is a tree, for which the demographic processes of growth, mortality, and regeneration are simulated. Processes at the stand and landscape scale constrain the dynamics of individual trees and thus allow for a robust scaling of tree-scale processes to large areas (Seidl et al., 2012a).

iLand integrates an agent-based model of forest management (Rammer and Seidl, 2015) in which general stand treatment programs (i.e., a sequence of management interventions carried out over the course of stand development) are dynamically adapted to the forest state emerging from the simulation. We here applied a single stand treatment program implemented by a sole agent across the entire study landscape. Stand treatment programs included planting after harvests or natural disturbances based on prescribed planting schemes, thinning operations, harvesting and post-disturbance salvaging. In addition to stand-level management the model also includes a landscape-level scheduling module that aims for equally distributed annual harvests (e.g., by re-scheduling other planned activities in response to salvage harvesting) and accounts for spatial contingencies.

iLand simulates forest disturbances in a spatially explicit manner (Seidl et al., 2014a; Seidl and Rammer, 2017). Wind disturbances are initiated by the wind speed of severe wind events provided as external input to the simulation. The model initiates wind disturbances in locations, where canopy rugosity changes abruptly, i.e., where vertical differences between the top heights of neighbouring grid cells exceed 10 m (e.g. Blennow and Sallnäs, 2004). Next, wind speed at the canopy top height is calculated based on a vertical wind profile at the stand edge (Gardiner et al., 2000), and individual-tree turning coefficients (Hale et al., 2012) are calculated. The latter two information are used to calculate the critical wind speeds for uprooting and tree breakage based on the approach of Gardiner et al. (2000). If the soil is frozen, only the stem breakage is allowed to occur. The final evaluation of the impact of wind on forest is based on comparison of the prevailing wind speed to the critical windspeed; if the critical wind speed is exceeded, the tree is broken or uprooted. The disturbance impact is simulated iteratively, with forest structure (including the appearance of new edges) being updated after each iteration if breakage or windthrow was simulated.

The process-based implementation of bark beetle disturbances considers bark beetle phenology and development, spatially explicit dispersal of beetles, colonization and tree defence, as well as temperature-related overwintering success (Seidl and Rammer, 2017). Large outbreaks are typically triggered by wind disturbance, but smaller outbreaks occur also independently based on a climate-sensitive background probability. Bark beetle development is simulated based on the beetle phenology model by Baier et al. (2007). The model tracks beetle cohorts rather than individuals, with a cohort being defined as the minimum number of beetles needed to successfully colonize a tree. Every brood tree disperses a number of beetle cohorts determined by the reproductive rate of the beetle (Wermelinger and Seifert, 1999). Attacking beetle cohorts need to first overcome the defence system of the tree, which is approximated by its dynamically simulated non-structural carbohydrate reserves. The tree can be attacked in multiple waves of beetle cohorts in one vegetation period if the climate allows for the development of multiple beetle generations per years.

The model was tested and evaluated across a range of ecosystems in Europe and North America in previous studies (Seidl et al., 2012b; Silva Pedro et al., 2015; Thom et al., 2017a). A detailed evaluation of simulated productivity, natural mortality and regeneration patterns for the landscape studied here was conducted by Dobor et al. (2018). All tests showed satisfactorily performance of the model in the current study region.

2.2. Study landscape

The study landscape Goat Backs Mts. is located in central-eastern Slovakia (Lon 20.088 – 20.275, Lat 48.920 – 49.061) and covers an area of 16,050 ha (Fig. 1). The forest cover is 70%, dominated by Norway spruce, which makes up 75% of the forested area. Other important tree species are European larch (*Larix decidua* Mill.), Scots pine (*Pinus sylvestris* L.), Silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.). The elevation range is 620–1550 m a.s.l. 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 calcareous bedrock which dominates the highest reaches of the landscape.

The current silvicultural system is an even-aged management regime with a rotation length of approximately 100 years. The primary approach to tree regeneration in stands with fir and/or beech admixtures is a uniform shelterwood cut (Fig. 1). The shelterwood system contains 3–4 regeneration cuts applied over a period of approximately 30 years, followed by a final cut. In spruce monocultures, a small-scale clearcutting system is applied (cut-block size < 3 ha).

Wind and bark beetles (mainly *Ips typographus*) are the main agents of natural disturbance in the region. Over the last 20 years, the landscape has been subject to heavy windthrow and high severity bark beetle disturbance, affecting almost 40 percent of the study area (Dobor et al., 2018). Management responses to natural disturbances contain salvage logging of both wind and beetle-killed trees, and sanitation logging aimed to reduce the spread of bark beetles.

2.3. Vegetation, soil and climate data

We initialized the vegetation of the study landscape in iLand based on stand-level data from forest management plans (FMP) provided by the National Forest Centre of Slovakia. The data were collected in the field and contain attributes such as stand structure, species- and cohort-specific mean stand height and diameter, standing volume, site index, mean stand age and stand density.

Soil depth and plant available nitrogen – which are both important soil parameters for the simulation with iLand – were derived on a 100 × 100 m grid from the national forest soil database (National Forest Centre, Slovakia). Because soil depth was only available as categorical variable, depth information for each stand was sampled from a uniform distribution centred on the mean soil depth of each of the five depth categories. The soil database contained a relative nutrient content (0–1), which was used to estimate the plant-available N (kg m^{-2} $year^{-1}$) based on iLand-internal model logic (Seidl et al., 2012a).

Two types of climate data were used to drive the simulations. A stationary reference climate series was created based on daily meteorological data from a nearby meteorological station (Poprad-Gánovce, Slovak Hydrometeorological Institute), and spatially expanded to the study landscape using MTClim in combination with topography information (Hungerford et al., 1989; see Dobor et al., 2018 for details). A reference climate series was generated by randomly sampling years with replacement from the period 1996–2016. Future climate was

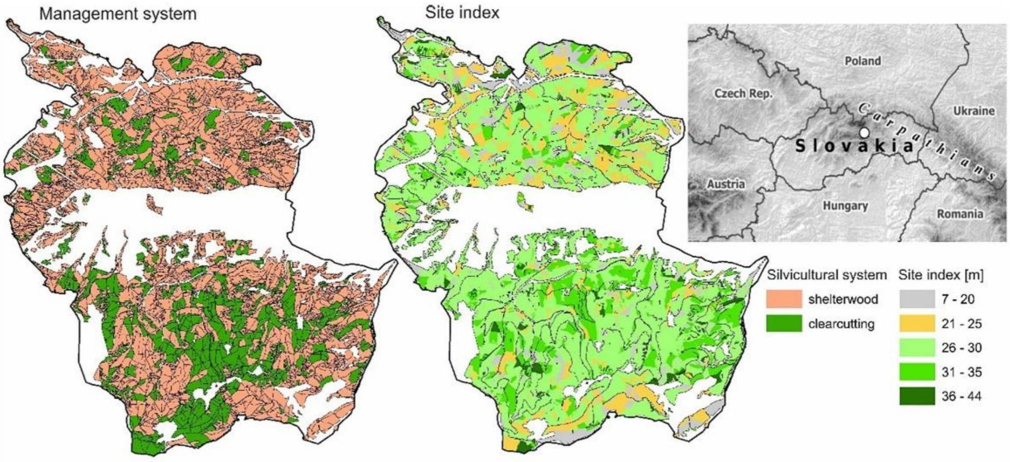

Fig. 1. Silvicultural systems applied in the study region (left). Clearcutting system is applied in pure stands of Norway spruce. Shelterwood system is applied in mixed stands. Site index map, with site index denoting the mean stand height at the age of 100 years (right). The insert shows the location of the study landscape in Central Europe (white circle).

Table 1
Indicators used to study the effect of a reduced rotation length on the forest ecosystems. All indicators were calculated as landscape-level averages, and changes are relative to the current rotation length (U_{def}).

Type of effect	Indicator [% change]
Main effect	Mean forest age
	Regular timber volume harvested (excluding salvage logged timber)
	Growing stock affected by wind
	Growing stock affected by bark beetles
Collateral effect	Mean stock of the total landscape carbon
	Abundance of large trees (DBH above 60 cm)
	Tree size diversity index (H index)
	Shannon diversity of tree species
	Rao's Quadratic Entropy Index of tree species shade tolerance

represented by seven GCM-RCM combinations driven by two Representative Concentration Pathway (RCP) scenarios (RCP4.5 and RCP8.5; Moss et al., 2010) (Appendix A). The data were developed in the framework of the CORDEX project (Giorgi et al., 2009). CO_2 concentrations used to drive the forest simulations were defined by the two RCP scenarios, and reached 538 ppm and 936 ppm in 2100 under RCP4.5 and RCP8.5 runs, respectively. Climate data driving the simulations after 2100 were sampled with replacement from the period 2080–2100 for each RCM, while CO_2 concentration was held at the level of 2100.

2.4. Simulation design

Prior to scenario simulations a 920-year spin-up run was performed to estimate the initial litter, dead wood and soil C pools, as well as to initialize stand structures (including individual tree positions) in a manner that is consistent with the internal logic of the model. The procedure used ('legacy spin-up') assimilates information on the current vegetation (here taken from FMP) in order to ensure that the resulting initial vegetation state for simulation is (i) consistent with the model-internal logic and (ii) represents the current structure and composition of the forest (see Thom et al. 2018 for details). Specifically, spin-up simulations are continuously compared to FMP reference data, and simulated management is dynamically adapted to ensure convergence between the simulation and the data at the level of individual stands. This approach accounts for the fact that the details of past land-use are often unknown, and ensures that the initial conditions of the simulation are in good correspondence with observations (e.g., with regard to structural legacies, Thom et al., 2018). The first 800 years of the spin-up included regular forest management operations but no natural disturbances. In a second 120-year spin-up phase, we allowed several low-intensity wind and bark beetle disturbances to ensure a smooth transition between the spin-up and scenario runs. The scenario simulations were run for 200 years, and each scenario was replicated 10 times to account for the stochasticity in the simulations.

The wind speed of simulated wind events was prescribed in the scenario simulations, with speed values sampled from a distribution parameterized based on past meteorological observations from the nearby meteorological station. In total, six wind events with the duration of 60 min were prescribed to occur during the 200-year simulation period. This series of wind events caused an average annual wind damage of 1.68–1.79 $m^3\ ha^{-1}\ year^{-1}$ (range of the 10 replicate simulations) under the default rotation length and the reference climate. This level of wind damage corresponds well with the long-term range of 0.9–2.2 $m^3\ ha^{-1}\ year^{-1}$ reported for Slovakia in the national forest disturbance statistics (Konôpka et al., 2016).

We note that while the occurrence of strong winds was prescribed, their impact on the forest ecosystem was simulated as an emergent property of the process-based wind model implemented in iLand (Seidl et al., 2014a). Also bark beetle disturbances were simulated dynamically, based on the iLand bark beetle module (Seidl and Rammer, 2017). A 60% salvaging intensity was applied in all simulations (see Dobor et al., 2020, 2019 for details on the implementation of salvage harvesting).

2.5. Rotation length experiment

The starting point for our analyses of rotation length effects was the default management currently implemented in the study region, as defined by national forestry legislation. The average rotation length (U_{def}) was 100 years for spruce stands, and 115 years for broadleaved species. The rotation age varies across the landscape, acknowledging a negative correlation of rotation length with site fertility. In addition to U_{def}, we simulated four alternative scenarios, reducing the rotation length of each stand by 10, 20, 30 and 40% (U_{red10}, U_{red20} U_{red30} and U_{red40}, respectively) relative to U_{def}. The rotation length was, however, not allowed to be $<$ 60 years. All reduced rotation length and U_{def} simulations were run both under reference climate and climate change.

The transition phase to a shorter rotation length can – depending on the speed of the transition – generate different undesired effects (e.g., temporary increase in harvested timber, increased occurrence of cleared areas, rapid change in forest demography affecting biodiversity, etc.). To study realistic trajectories, we thus simulated a relatively long transition period of 30 years.

We distinguished two broad groups of effects of shortened rotation length in our analysis, which we refer to as main effects (i.e., those primarily discussed by managers in the context of rotation length) and collateral effects (i.e., those that are not receiving broad attention in the management community, yet might also be important when making management decisions) (Table 1). Main effects include the modification of forest age, the amount of harvested wood, and the level of disturbance by wind and bark beetles. As collateral effects, we focused on two different groups of indicators, representing forest carbon stocks and biodiversity. In particular, we evaluated effects on total landscape carbon storage, tree size diversity, the abundance of large trees, tree species diversity and tree shade tolerance diversity. Tree species diversity was evaluated based on the Shannon entropy index (Shannon, 1948) using basal area shares. Shade tolerance diversity was evaluated based on the Rao's Quadratic Entropy (Ricotta and Szeidl, 2009) using shade tolerance ratings of the tree species occurring on the landscape. The shade tolerance ratings were based on Niinemets and Valladares (2006) with minor modifications for consistency with iLand framework (http://iland.boku.ac.at/species + parameter). We used shade tolerance ratings as they are a good proxy for the different successional roles of tree species in forest dynamics (e.g., early vs. late seral species), and thus capture an important component of functional diversity beyond the tree species richness and abundance. The Rao's Quadratic Entropy was calculated as

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j$$

where d_{ij} is the dissimilarity between species i and j (here the absolute difference between species shade tolerance scores; note that d_{ij} is normalized between [0,1] by dividing it by the maximum difference between the species represented in the landscape), p_i and p_j are the relative proportions of species i and j. We used R package SYNCSA (Debastiani, 2020) for this analysis.

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

$$H_{size} = \frac{H_{DBH} + H_H}{2}$$

$$H_{DBH} = -\sum_{i=1}^{N_{DBH}} p_i \ln(p_i)$$

$$H_H = -\sum_{i=1}^{N_H} p_i \ln(p_i)$$

$$p_i = \frac{g_i}{G}$$

where N_{DBH} and N_H are the number of DBH and height classes present in the landscape, g_i is the basal area (m^2) of DBH or height class i, and G is the basal area of the landscape (m^2). We used 5-cm classes for DBH and 2-m classes for height (Cordonnier et al. 2013) with a minimum values of 4 m height and 5 cm DBH.

Although there is ample evidence that structural complexity and the abundance of microhabitats (cavities, dead branches) increase with tree diameter, the thresholds for identifying valuable habitat trees differs widely between authors and ecosystems (e.g. Larrieu et al., 2012; Larrieu and Cabanettes, 2012). We here applied a 60 cm diameter threshold for identifying large trees, following a suggestion of Lachat and Butler (2007) for mixed forests.

For all indicators we evaluate the effect of shortened rotation length and the modulation of this effect by climate change. To do this, we compare simulations under different levels of shortened rotation against simulations under U_{def}. The compared pairs of simulations are always driven by the same climate scenario, i.e. reference climate and climate change projections.

For all collateral effects and the harvested volume, we separately analysed the short-term (average over the first 30 years of the simulation) and the long-term (average over the remaining 170 years of the study period) effects of shortening rotation lengths. For the disturbed growing stock, we analysed the 200-year averages only, because 30 years were too short to make robust assessments of the highly stochastic disturbance events. We report the median and 10 – 90% quantile range over the 14 simulated climate change scenarios and 10 replicates.

3. Results

3.1. Main effects of reduced rotation

3.1.1. Forest age

The average forest age during the 200-year simulation period was 61 years under U_{def} and reference climate (Table 2). Average forest age decreased by up to 18% (11 years) under the most extreme scenario U_{red40}. Because of the uneven distribution of current forest ages (resulting from past natural disturbances), forest age fluctuated regularly throughout the 200-year study period. The frequencies of this fluctuation roughly equalled the respective rotation age being simulated (Fig. 2ab). Climate change resulted in a higher amplitude of age variation over time, while conserving the general pattern also observed under reference climate.

3.1.2. Harvested volume

Reducing rotation length increased the amount of harvested wood volume (Table 2). In the short-term (i.e., the first 30 years of the simulation), this increase ranged between 35% and 92% of the harvest levels reached under U_{def}, depending on the intensity of reduction (U_{red10} – U_{red40}) (Fig. 3). In the long-term (i.e. over the remaining 170 years of the simulation), the initially strong effect on harvested volume was reduced. Under U_{red40}, for instance, the long-term harvest level increase was 22% (i.e., a change from 6.7 to 8.1 $m^3ha^{-1}year^{-1}$) (See Fig. 4).

Climate change increased the overall amount of harvested wood volume from 6.8 to 7.6 $m^3ha^{-1}year^{-1}$ (200-year average under U_{def}). The relative effects of reduced rotation on harvested volume did not change under climate change (Fig. 3, Table 2). The temporal evolution of harvested volumes was more erratic under climate change than under reference climate (Appendix C).

3.1.3. Wind and bark beetle disturbances

The level of natural disturbance decreased with shorter rotation lengths (Table 2). The average level of growing stock affected by wind and bark beetles under U_{def} was 3.8 m^3 ha^{-1} $year^{-1}$ under reference climate, and 5.7 m^3 ha^{-1} $year^{-1}$ under climate change (i.e. an increase by 50%) (Table 2). Climate change doubled bark beetle disturbances (from 2.2 to 4.5 m^3 ha^{-1} $year^{-1}$), while wind disturbance decreased from 1.7 to 1.2 m^3 ha^{-1} $year^{-1}$. Reducing the rotation length decreased the total disturbance by up to 14% under reference climate, but only by 6% under climate change (average change over simulations driven by all 14 climate scenarios). Reduced rotation buffered the impact of wind more effectively than the impact of bark beetles (-18% vs. −12% under reference climate, and −25% vs. −0.7% under climate change in the $U_{red40\%}$ scenario).

3.2. Collateral effects of reduced rotation length

Reduced rotation length decreased the total amount of carbon stored in the landscape (Table 3). This effect was pronounced in the short-term (up to −7% under U_{red40}), while the long-term effect was −2% only. Climate change had a generally positive effect on forest carbon storage (Appendix C), but slightly amplified the negative effect of reduced rotation length (long-term effect of up to −3%) (Fig. 5, Table 3). However, the negative effects of reduced rotation length on carbon storage decreased over time, with U_{red} and U_{def} trajectories converging after 150 simulated years (Appendix B).

Mean tree size diversity index H was 2.23 during the first 30 years of the simulation and 2.50 during the remaining 170 years. H increased in response to a reduced rotation length, with the increase being more pronounced in the short-term (up to 4.5%) than in the long-term (up to 2.5%). The effect of climate change on the rotation length response of H was negligible (Table 3). Reduced rotation decreased the number of large trees in the short-term by 20% under U_{red40} (from 34 to 27 trees ha^{-1}) in both the reference and climate change scenarios. The effect was more pronounced in the long-term, when the number of large trees decreased by 30 and 32% under reference climate and climate change, respectively (from 27 and 26 trees ha^{-1} to 19 and 18 trees ha^{-1}).

Both tree species diversity and diversity in shade tolerance increased strongly during the simulation period as disturbances and harvesting opened up the canopy of the initial mature forest dominated by Norway spruce. In the long-term and under the reference climate,

Table 2

The direct effects of reducing rotation length. Averages over the entire simulation period are shown. Each value shows the average of 10 simulation replicates. In case of climate change, also 14 climate scenarios are averaged. RC: reference climate, CC: climate change.

Indicator	Absolute values			Differences from default rotation [%]							
	Unit	Default rotation		U_{red10}		U_{red20}		U_{red30}		U_{red40}	
		RC	CC	RC	CC	RC	CC	RC	CC	RC	CC
Age	years	60.6	58.3	−8.0	−7.3	−13.7	−12.7	−15.7	−16.7	−18.1	−20.1
Harvested volume	m^3 $ha^{-1}year^{-1}$	6.8	7.6	9.9	7.1	21.8	18.2	27.8	25.9	32.8	32.1
Wind	m^3 $ha^{-1}year^{-1}$	1.7	1.2	−10.6	−10.2	−18.2	−18.5	−18.3	-22.7	−17.9	−24.8
Bark beetles	m^3 $ha^{-1}year^{-1}$	2.1	4.5	−5.2	0.1	−10.6	0.1	−9.3	1.0	−11.5	−0.7
Total killed	m^3 $ha^{-1}year^{-1}$	3.8	5.7	−7.6	−2.2	−14.0	−4.0	−13.3	−4.1	−14.3	−5.9

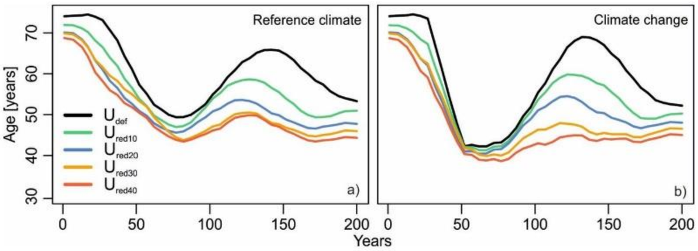

Fig. 2. Temporal development of mean forest age on the study landscape under the default rotation age (U_{def}) and different levels of reduced rotation (U_{red}). A moving-window smoothing (k = 25) was applied on the age time series for presentation purpose. Each line shows the average of 10 replicated simulations. In case of climate change, also 14 climate scenarios were averaged.

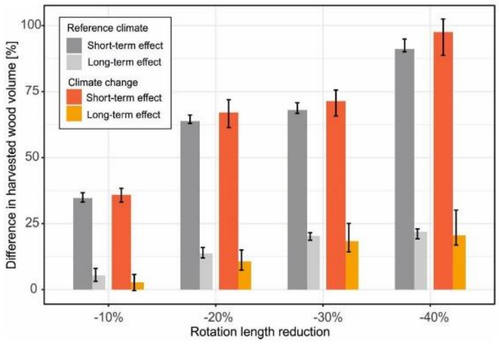

Fig. 3. Effect of reduced rotation length on the amount of harvested wood volume, expressed as percent difference relative to the default rotation. Short-term (average over the first 30 years of simulation) and long-term (average over the remaining 170 years of the study period) effects are shown. Columns show median values of replicated simulations and different climate change scenarios. Whiskers indicate 10 to 90% quantile range.

reduced rotation length had almost no effect on these two indicators. In the short-term, however, the two species diversity indicators increased slightly in response to the high harvesting intensity in the first decades of the simulation. Climate change increased Shannon and Rao's diversity in the long-term, while the short-term values remained similar to reference climate levels. Overall, the sensitivity of species and shade-tolerance diversity to reduced rotation was small.

4. Discussion

Addressing natural disturbances is an increasing concern for forest management in Europe, particularly due to a recent increase in disturbance activity and the propensity for further amplification of disturbance regimes under climate change (Seidl et al., 2014b; Senf et al., 2018). Yet, the efficiency of frequently discussed disturbance management measures remains insufficiently understood, and it is unclear whether past practices will retain their leverage also under future environmental conditions (e.g. Dobor et al. 2020). Furthermore, potential collateral effects of disturbance mitigation measures need to be considered, yet are rarely quantified comprehensively in studies focusing on disturbance management. We here show that a reduced rotation length can substantially reduce the impact of wind and bark beetle disturbances, but also highlight a decreasing efficiency of the measure under climate change. Furthermore, collateral impacts of reduced rotation lengths on forest biodiversity and carbon cycling indicators persisted.

4.1. Potential and limitations of reduced rotation lengths

4.1.1. Potential for reducing disturbances

We showed that shortened rotation lengths reduce the share of mature trees on the landscape and lower the risk of wind and bark beetle disturbances. Rotation reduction by 40% (i.e. the most severe variant studied here) reduced forest age by 18%, and decrease the total amount of disturbed growing stock by 14% under the reference climate.

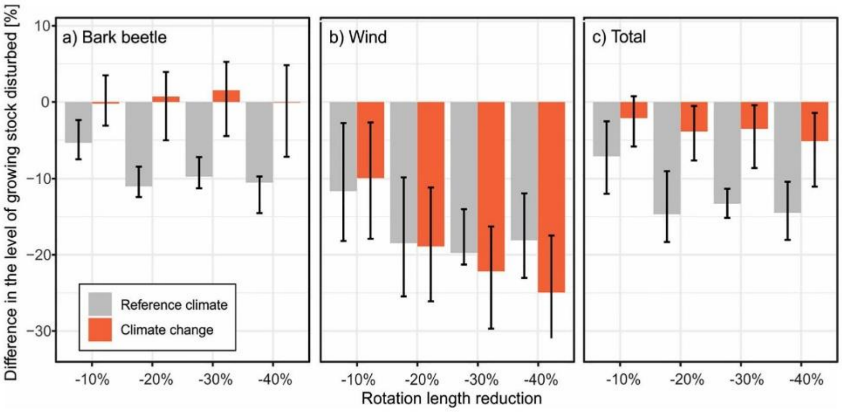

Fig. 4. Effect of reduced rotation length on the level of disturbance by wind and bark beetles, expressed as the percent difference relative to the default rotation. Averages over the 200-year simulation period are shown. Columns show median values of replicated simulations and different climate change scenarios. Whiskers indicate 10 to 90% quantile range.

Table 3
Indicator values for the collateral effects of reduced rotation length. Pairs of values indicate the short-term effects (upper value; average over the first 30 years of simulation) and the long-term effect (bottom value; average over the remaining 170 years). The values are averages over 10 replicate simulations. In case of climate change, also the 14 climate scenarios are averaged. RC: reference climate, CC: climate change.

Indicator	Absolute values			Differences from default rotation [%]							
	Unit	Default rotation		−10%		−20%		−30%		−40%	
		RC	CC	RC	CC	RC	CC	RC	CC	RC	CC
Landscape carbon	tC ha^{-1}	420	423	−2.9	−2.8	−5.1	−5	−3.9	−3.8	−6.5	−6.3
		421	453	0.1	−0.5	−0.8	−1.4	−1.4	−2.4	−2	−3.3
Large trees	no ha^{-1}	33.8	33	−10.2	−10.2	−17.5	−17.2	−14.2	−13.9	−20.1	−19.7
		27	26	−11.2	−11.4	−20.8	−19.5	−26.2	−27.3	−30.2	–32.1
Structural diversity index (H)	–	2.23	2.24	2.1	2.1	3.5	3.5	3.2	3.1	4.5	4.3
		2.5	2.52	0.9	0.6	1.7	1	2.2	1.3	2.5	1.6
Shannon diversity index	–	0.25	0.25	0.9	0.9	1.9	2.0	1.9	1.9	3.6	3.7
		0.04	0.13	−3.2	−0.2	−2.8	0.3	−2.1	0.3	0.2	1.0
Rao's Quadratic Entropy Index	–	0.35	0.36	0.3	0.3	1.1	1.1	1.2	1.3	2.9	2.9
		0.44	0.52	−3.0	0.3	−2.9	1.5	−2.2	2.4	0.0	3.8

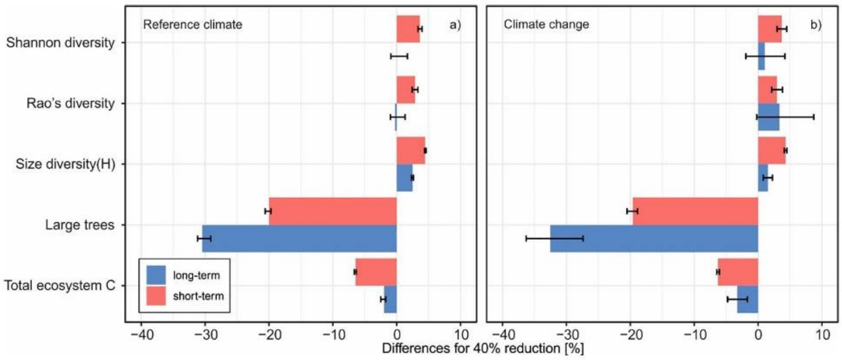

Fig. 5. Collateral effects of a 40% reduction in the current rotation length. Short-term (over the first 30 years of simulation) and long-term (over the remaining 170 years of the study period) effects are presented. Columns show median values of replicated simulations and different climate change scenarios. Whiskers indicate 10 to 90% quantile range.

Climate change increased the amount of disturbed growing stock by 50% mainly due to increased bark beetle outbreaks, and reducing the rotation length was not able to fully compensate this increase. Overall, the relative effect of reduced rotation length on disturbances decreased with climate change from 14 to 6% under the U_{red40}. Our results thus suggest that expectations of lowered vulnerability of forest ecosystems to disturbances under climate change via reduced rotation lengths need to be reconsidered (e.g. Eidmann 1992, Björkman et al. 2015). This finding is in line with previous research indicating a decreasing efficiency of conventional disturbance management measures under climate change (Dobor et al., 2020, 2019). Overall, our study provides further evidence that controlling forest disturbances is increasingly challenging under climate change, underlining the growing relevance of alternative management approaches such as fostering resilience (i.e. strengthening the ecosystems ability to tolerate disturbances without changing substantially, and recover rapidly from them) (e.g. Seidl, 2014).

The fact that reduced rotation lengths decrease wind risk have been reported previously (Kuboyama and Oka, 2000; Moore and Quine, 2000). This effect mainly results from a reduced length that trees are exposed to extreme winds, and a smaller share of tall trees on the landscape, which are particularly predisposed to wind breakage or uprooting (Gardiner et al., 2000; Jactel et al., 2009). Quantitative evidence for positive effects of shortened rotation lengths remain, however, scarce for bark beetles (but see Taylor and Carroll, 2004; Whitehead et al., 2004 for *Dendroctonous ponderosae*). Nonetheless, research on the ecology (e.g. Wermelinger, 2004) and infestation patterns of *Ips typographus* clearly identified a preference of the beetle for older, larger diameter trees (Hlásny and Turčáni, 2013; Netherer et al., 2019; Netherer and Nopp-Mayr, 2005). In this regard an interesting finding of the current study is that reduced rotation lengths dampen wind disturbances more efficiently than bark beetle disturbances (-18% vs. −11% under $U_{red40\%}$, relative to the default rotation). This suggests that a critically large number of suitable host trees remains on the landscape even under a 40% reduction in the rotation length. This difference was even greater under climate change (-25% vs. −0.7%), underscoring that under the elevated bark beetle population levels of the future, even isolated patches of potential host trees are increasingly at risk (Honkaniemi et al., 2020). It is important to note, however, that wind and bark beetle dynamics are intricately linked in Central European forests (Marini et al., 2017; Stadelmann et al., 2013), not least because they "compete" for the same resource, i.e. mature trees. For example, Dobor et al. (2019) found that the intense suppression of bark beetle disturbances increased the share of dense and mature forests on the landscape, which subsequently increased the susceptibility to wind disturbance. Conversely, an increased impact of bark beetles due to climate change may result in a concomitant decrease in wind impact, as observed here. We conclude by highlighting that the current study is the first to explore the dynamic relationships between multiple interacting disturbance agents and rotation length under climate change. Our analysis thus considerably improves the understanding of the potential future efficiency of important disturbance management measures.

A key limitation of our analysis is the sole focus on wind and bark beetle disturbances, which are both positively related to older trees. A number of other important agents of tree mortality particularly affect young trees, and could thus be hypothesized to increase with decreasing rotation length. These include important pests such as the pine weevil *Hylobius abietis* (Leather et al., 1999), but also abiotic drivers such as increasing drought (Kolb et al., 2016). Furthermore, the edges created by shortened rotation length as well as mechanical damage from harvesting operations could further increase the susceptibility of trees to disturbance (Buras et al., 2018; Rönnberg, 2000; Woodcock et al., 2015). Climate change could further amplify these effects (Allen et al., 2010; Inward et al., 2012), which highlights the need to study the effects of reduced rotation length on tree mortality more comprehensively in the future.

4.1.2. Limitations arising from collateral effects

The choice of rotation length has manifold impacts on forest soils, carbon, biodiversity, non-wood forest products and timber production (Felton et al., 2017; Kaipainen et al., 2004; Roberge et al., 2016). Therefore, even though the decision to shorten the rotation length can be motivated by the prospect of reducing natural disturbances, its effects on other management objectives need to be considered. Mitigating climate change is increasingly recognized as an important objective for contemporary forestry (Canadell and Raupach, 2008; Luyssaert et al., 2018) and management should thus consider the effects of interventions on forest carbon stocks and sink strength (Pilli et al., 2016). We found that reduced rotation can be in conflict with this objective, particularly in the short term. This finding is in agreement with previous studies which reported mostly negative effect of shortened rotation lengths on forest carbon (Kaipainen et al., 2004; Liski et al., 2011; Lundmark et al., 2018). We note, however, that an initial decrease in landscape carbon storage can be offset by increased carbon storage in the wood products pool, and positive substitution effect are possible from increased timber use (Lamers et al., 2014). Future works should therefore consider the carbon cycle effects of management more broadly, accounting for impacts on the entire forestry sector (Lundmark et al., 2018; Seidl et al., 2008). Managing forest carbon under climate change also needs to consider an ameliorative effect of increased CO_2, which is an important driver of the current global carbon sink (Bellassen and Luyssaert, 2014). In our simulations, this effect caused an overall increase in forest carbon storage under climate change, and compensated carbon loss due to reduced rotation lengths (Appendix C) (see also Dobor et al., 2018). However, experimental evidence of the persistence of a CO_2 fertilization effect is limited (Lindner et al., 2014) and trade-offs with other climate change impacts on forest demography are likely (McDowell et al., 2020).

Growing interest in reducing forest rotation lengths has also raised concerns about potential effects on biodiversity, especially since big old trees and structurally complex overmatured forests provide important habitat for a wide range of species of conservation concern (Hilmers et al., 2018; Lassauce et al., 2013). This effect is important as production forests are increasingly recognized to also play an important role in the conservation of biodiversity (Díaz-Rodríguez et al., 2012; Felton et al., 2017). Here we show that a 40% reduction in rotation length resulted in a 30% decrease in large trees. These effects could possibly be compensated by retention forestry practices (Gustafsson et al., 2012), promoting the retention of trees in harvested areas and mimicking natural disturbance regimes in harvesting patterns (Lassauce et al., 2013; North and Keeton, 2008). Another approach to compensate for potential negative effects of shortened rotation length in managed forests could be the increase of protected areas on the landscape (Felton et al. 2017). While the effects of a shortened rotation length negatively impacted the prevalence of large trees, tree species diversity as well as the diversity in different functional groups (light demanding vs. shade tolerant) increased. The increase in harvesting intensity resulting from a reduced rotation length thus accelerates the transformation of structurally and compositionally homogenous forests to more diverse conditions, similarly to the catalysing effect of natural disturbances (Thom et al., 2017b). This effect can be potentially beneficial from the perspective of climate change adaptation (Bouriaud et al., 2015), facilitating necessary transformations.

Despite the fact that this is – to our knowledge – the most comprehensive study on the multiple simultaneous effects of reduced rotation length to date, shortening the rotation length might also affect important indicators not considered here. Reduced rotation periods do, for instance, increase the exposure of soils to sun and rain, and could thus result in soil loss via erosion and elevated decomposition (Kreutzweiser et al., 2008). Furthermore, an increased frequency of harvests could reduce the protective effect of forest ecosystems against natural hazards such as debris flow events and floods (Sebald et al., 2019). A higher harvesting frequency and smaller tree dimensions could also have negative impacts on the recreational value of forest ecosystems (Curtis, 1997). This underscores the need for a broad and comprehensive assessment of potential collateral effects of forest management decisions before they are implemented.

4.2. Conclusions

Reduced rotation length is increasingly discussed as an important component of adapting managed forests to climate change (Bolte et al., 2009; Lindner et al., 2010), in particular addressing changing disturbance regimes (Gardiner and Quine, 2000; Jactel et al., 2009). In contrast to other adaptation measures with long lead times, such as changing the tree species composition (e.g. Keenan 2015), the effects of reduced rotation lengths can be obtained within a relatively short period of time. Such approaches are increasingly needed because proactive and anticipatory adaptation actions to climate change have been neglected in many regions of Europe (Sousa-Silva et al., 2018), and climate change is progressing at an accelerating rate.

Here we show that the reduction of forest rotation length is an important tool for managing natural disturbances in Central Europe. However, our analyses also clearly demonstrate that the efficiency of reduced rotation lengths to counter increasing disturbances is limited, and that the negative effects of climate change cannot be fully compensated by shortening the rotation length. Transitions towards shorter rotation lengths also generated a number of undesired effects on ecosystem services and biodiversity. We thus conclude that reducing rotation lengths needs to be applied with caution, evaluating its positive and negative implications in the context of the local conditions and objectives. While we here simulated simultaneous rotation length reductions across an entire landscape we note that spatially stratified approaches to risk management, i.e., considering landscape heterogeneity and the differential risk of stands within a landscape, hold high potential to maximize outcomes while minimizing undesired effects (Dobor et al., 2020; Seidl et al., 2018). Furthermore, reducing the rotation length is only one possible option to address increasing disturbances, and should be applied in concert with other disturbance management approaches such as fostering disturbance resilience (Hlásny et al., 2019; Seidl, 2014). We conclude that addressing changing climate and disturbances regimes remains a major challenge for forest management in Central Europe, and while shortened rotation lengths can make a potential contribution, they are no silver bullet solution.

CRediT authorship contribution statement

Soňa Zimová: Data curation, Formal analysis. **Laura Dobor:** Methodology, Formal analysis, Writing - review & editing. **Tomáš Hlásny:** Methodology, Supervision, Writing - original draft. **Werner Rammer:** Software, Writing - review & editing. **Rupert Seidl:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Used climate model results and projected climate change

(See Table A1 and A2)

Table A1
Description of the used combinations of global and regional climate models.

	Global Climate Model		Regional Climate Model		
1	CM5A-MR	Institut Pierre-Simon Laplace, France (IPSL)	RCA4	Swedish Meteorological and Hydrological Institute, Rossby Centre, Sweden (SMHI)	Strandberg et al., 2014
2	CNRM-CM5	Météo-France / Centre National de Recherches Météorologiques, France (CNRM)	RCA4	Swedish Meteorological and Hydrological Institute, Rossby Centre, Sweden (SMHI)	Strandberg et al., 2014
3	EC-EARTH	Irish Centre for High-End Computing (ICHEC)	HIRHAM5	Danish Meteorological Institute, Denmark (DMI)	Christensen et al., 2007
4	EC-EARTH	Irish Centre for High-End Computing (ICHEC)	RACMO22E	Royal Netherlands Meteorological Institute, De Bilt, The Netherlands (KNMI)	van Meijgaard et al., 2008
5	EC-EARTH	Irish Centre for High-End Computing (ICHEC)	RCA4	Swedish Meteorological and Hydrological Institute, Rossby Centre, Sweden (SMHI)	Strandberg et al., 2014
6	MOHC-HADGEM2-ES	Met Office Hadley Centre, United Kingdom (MOHC)	RCA4	Swedish Meteorological and Hydrological Institute, Rossby Centre, Sweden (SMHI)	Strandberg et al.,2014
7	MPI-ESM-LR	Max Planck Institute for Meteorology, Germany (MPI)	RCA4	Swedish Meteorological and Hydrological Institute, Rossby Centre, Sweden (SMHI)	Strandberg et al.,2014

Table A2
Projected changes of temperature and precipitation in the growing season (April-September) for periods 2031–2060 and 2071–2100 based on six climate models and two RCP scenarios compared to the period 1996–2016.

	Expected changes for 2031–2060				Expected changes for 2071–2100			
Model	Temperature (IV-IX) [°C]		Precipitation (IV-IX) [%]		Temperature (IV-IX) [°C]		Precipitation (IV-IX) [%]	
RCP	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5
1	0.9	1.5	−18.0	−10.3	1.9	4.0	–22.3	−21.2
2	0.2	0.3	−21.6	−7.2	1.1	2.7	−16.6	−15.5
3	0.9	1.0	−12.8	−4.1	0.9	2.7	4.2	3.7
4	0.2	0.7	−3.4	−5.0	1.0	2.7	−2.9	−8.7
5	0.8	1.4	–22.9	−16.7	1.6	3.6	−14.9	−24.0
6	1.1	1.7	−13.9	−15.4	2.1	4.1	−15.1	–22.7
7	0.7	1.1	−18.1	−7.4	1.1	3.3	−21.8	−19.9

Appendix B. Simulated time series of differences from the default rotation

(See Fig. B1)

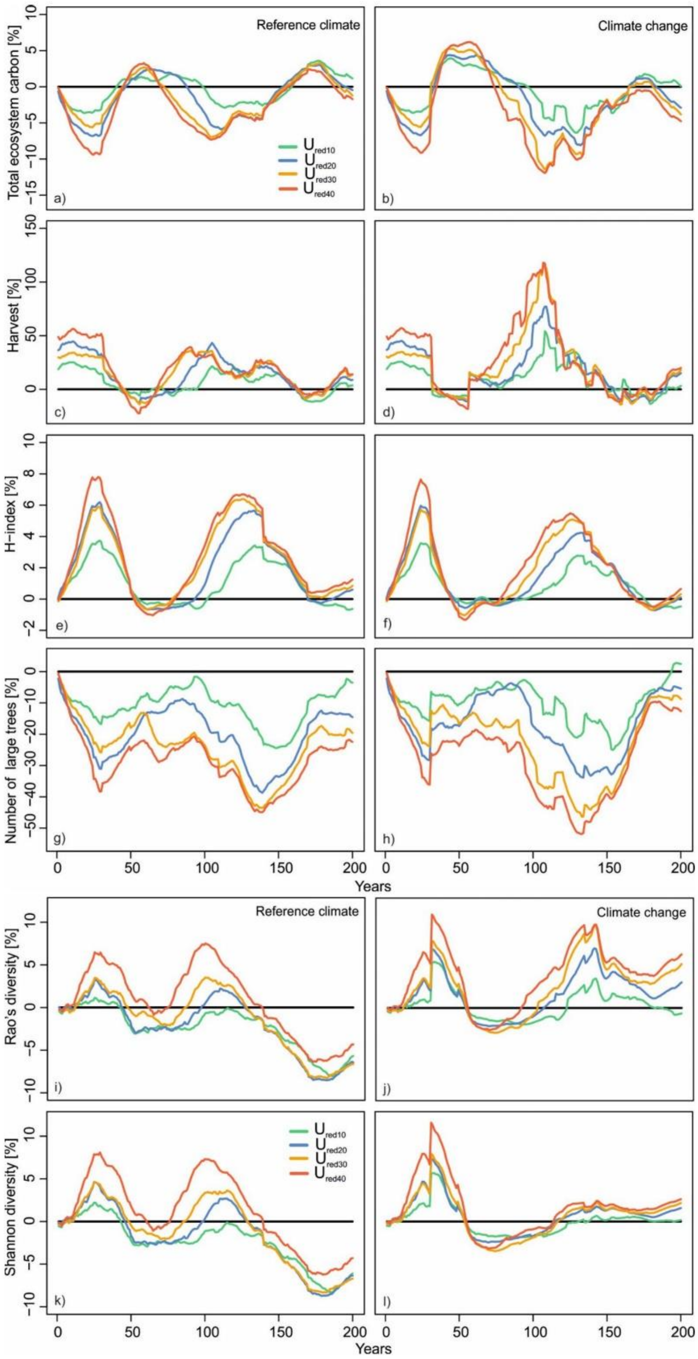

Fig. B1. Simulated time series of here tested forests development indicators. Relative differences of values reached under different levels of rotation length reduction (U_{red}) from the default rotation (U_{def}) are shown. The horizontal black line indicates the threshold of no difference from the default rotation.

Appendix C. Simulated time series of selected forest development indicators

(See Fig. C1)

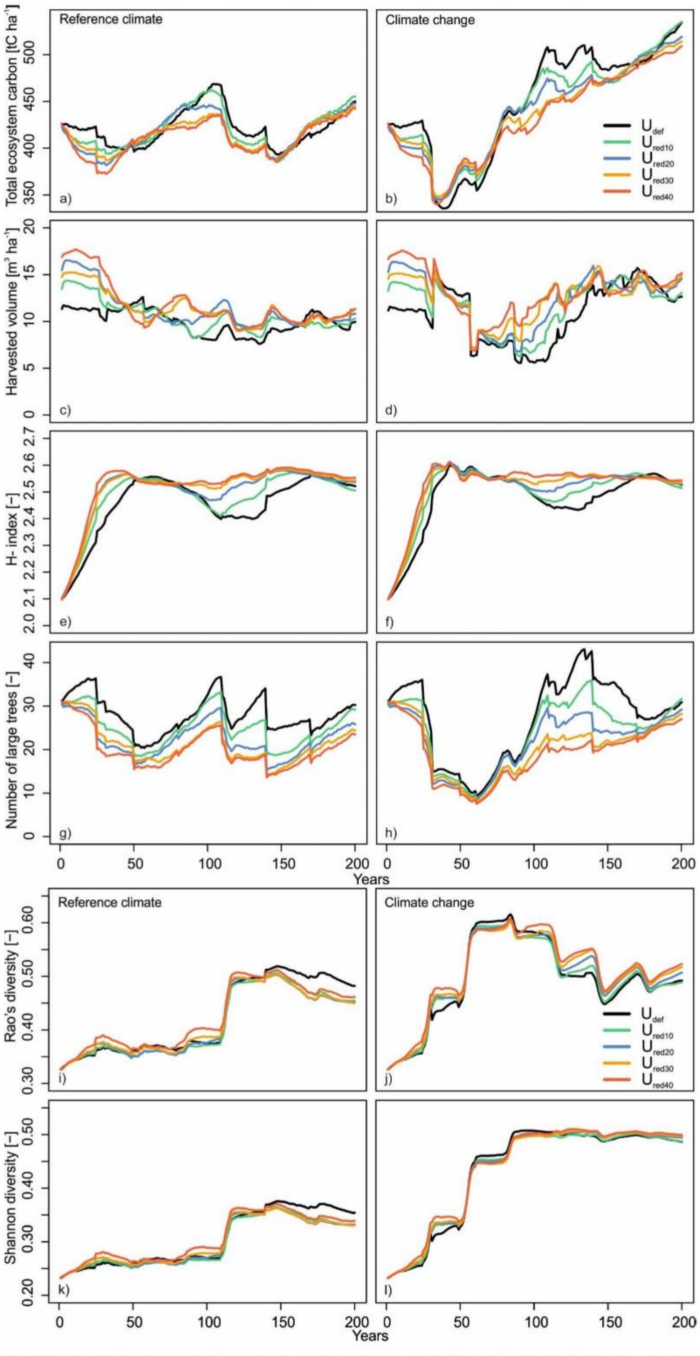

Fig. C1. Temporal evolution of selected forest development indicators in the study landscape under different levels of reduction (U_{red}) of the default (U_{def}) rotation period.

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5.2 Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks?

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Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks?

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Abstract

1. Salvage logging is one of most frequently applied management responses to forest disturbances world-wide. As forest disturbances are increasing, so too is the application of salvage logging, yet its effects on ecosystems remains incompletely understood. In the Norway spruce (*Picea abies* (L.) Karst.) forests of Europe, salvaging of windfelled trees is *inter alia* applied to reduce the risk of bark beetle outbreaks (mainly *Ips typographus* L.). By preventing further disturbances, salvage logging can conserve live tree carbon (C) in forest landscapes. At the same time salvage logging reduces C stocks in detrital pools via the extraction of disturbed trees, its net effect thus remains unclear.
2. We used the forest landscape model iLand to explore the effect of a wide range of salvaging intensities on (a) subsequent bark beetle outbreaks, and (b) landscape-scale forest C stocks in a Norway spruce-dominated production forest in Slovakia under past and future climatic conditions.
3. Climate change resulted in a two- to three-fold increase in bark beetle disturbances throughout the 21st century in our simulations. We found that removing >95% of disturbed trees can effectively buffer the effect of increasing disturbances, dampening bark beetle infestations and increasing live tree C. Total ecosystem C followed a U-shaped pattern over salvaging intensity, with highest values in no salvage and 100% salvage scenarios.
4. However, realistic rates of salvaging (<95% of disturbed trees detected and removed) had no significant effect on bark beetle dynamics and live tree C, and reduced the total ecosystem C stored in the landscape. Furthermore, the effect of reduced bark beetle disturbance under intensive salvaging was partly offset by increased wind disturbance.
5. *Synthesis and applications.* Clearing disturbed areas to prevent future disturbances from bark beetles and conserve live tree carbon should only be applied where very high salvaging rates are feasible (i.e. small and concentrated disturbances). Considering that changing disturbance regimes make high-intensity salvaging increasingly challenging, alternative disturbance management approaches need to be developed.

KEYWORDS
bark beetle disturbance, climate change, disturbance management, forest carbon, Norway spruce, process-based forest modelling, salvage logging, wind disturbance

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1 | INTRODUCTION

Stand replacing forest disturbances such as wind, insect outbreaks or fires and the management responses they trigger are among the most severe perturbations of ecosystem processes (Leverkus, Rey Benayas, et al., 2018; Lindroth et al., 2009; Seidl, Schelhaas, Rammer, & Verkerk, 2014). Disturbances are natural processes in forest ecosystems and are important drivers of ecosystem dynamics (Stephens et al., 2013; Thom, Rammer, Dirnböck, et al., 2017; Thom, Rammer, & Seidl, 2017a). They often facilitate biodiversity (Thom & Seidl, 2016), mitigate forest vulnerability to future disturbances (Seidl, Donato, Raffa, & Turner, 2016; Stephens et al., 2013), and foster autonomous adaptation of forests to rapidly changing environmental conditions (Kulakowski et al., 2017; Lamers, Junginger, Dymond, & Faaij, 2014; Thom et al., 2017; Thom, Rammer, & Seidl, 2017a). However, disturbances also alter biogeochemical cycles in ecosystems, including carbon (C), nutrients and water and reset natural forest succession (Dobor et al., 2018; Mikkelson, Dickenson, Maxwell, McCray, & Sharp, 2013; Seidl, Rammer, & Spies, 2014). Consequently, disturbances are often perceived negatively in managed forest because they compromise the provisioning of ecosystem services and can have negative impacts on the economy of communities depending strongly on revenue from forests (Rosenberger, Bell, Champ, & White, 2013). Humans have therefore applied strategies to mitigate the risk of disturbances for many decades (Roberge et al., 2016; Seidl, 2014). However, long-term disturbance prevention is not consistent with natural ecosystem dynamics (Holling & Meffe, 1996). Furthermore, efforts to prevent risk in the short term can result in increased mid- to long-term risks, for example via creating a high share of overmatured stands, high biomass stocks or simplified vertical and horizontal structure (Reyer et al., 2017).

Salvage logging is one of most widespread management responses to forest disturbances world-wide (Leverkus, Lindenmayer, Thorn, & Gustafsson, 2018; Leverkus, Rey Benayas, et al., 2018; Müller et al., 2018). Salvage logging is the felling and removal of trees in naturally disturbed forests with the primary intention to recoup economic losses, reduce hazards to infrastructure and ensure human safety (Molinas-Gonzáles, Leverkus, Marañón-Jimenéz, & Castro, 2017). Furthermore, in many ecosystems salvage logging also aims to fulfil a sanitary role, by reducing the risk from subsequent disturbances. In Norway spruce (*Picea abies* (L.) Karst.) forests, for instance salvage logging of windfelled timber is frequently aimed at removing broken or uprooted trees which serve as breeding substrate for native bark beetles (mainly *Ips typographus* L.) (Schroeder, 2007; Stadelmann, Bugmann, Meier, Wermelinger, & Bigler, 2013). Bark beetles swiftly colonize such trees because of their weakened defences (Komonen, Schroeder, & Weslien, 2011), and the corresponding population build-up triggers a transition from endemic to epidemic population dynamics (Kausrud et al., 2012), with beetles spreading into healthy forests around windthrown areas. This interaction effect can trigger large outbreaks of bark beetles, which—under favourable conditions—can substantially exceed the extent of the initial wind disturbance (Mezei et al., 2017; Økland, Nikolov, Krokene, & Vakula, 2016).

Recent increases in forest disturbances (Seidl, Schelhaas, et al., 2014; Senf et al., 2018) have led to an unprecedented increase in salvage logging (Leverkus, Lindenmayer, et al., 2018). However, salvage logging has tangible effects on biodiversity (Thorn et al., 2017) and can compromise mechanisms underlying ecosystem resilience (Ghazoul, Burivalova, Garcia-Ulloa, & King, 2015). Furthermore, concerns have emerged that salvage logging may affect cultural, regulating and supporting ecosystem services throughout the ecosystem services cascade (Leverkus, Rey Benayas, et al., 2018). In Europe`s spruce forests, one prominent example in the context of climate regulation is the effect of salvage logging on forest carbon (C) storage. Salvage logging reduces forest C storage by removing the C stored in disturbed trees, but can also enhance live tree C pools by dampening bark beetle outbreaks. Due to the complex interplay between these effects the impact of salvage logging on forest C stocks remains unclear. Moreover, salvaging affects multiple ecosystem processes and their interactions (Leverkus, Rey Benayas, et al., 2018), potentially resulting in non-additive outcomes. This is of particular concern in the context of climate change, as future outcomes of salvage logging could differ from the past due to nonlinear effects of changing environmental conditions. Climate change can, for instance increase the severity of bark beetle disturbances in their native range, facilitate the expansion of beetle populations to new locations (Cudmore, Björklund, Carroll, & Lindgren, 2010), and amplify the interactions between wind and bark beetles (Seidl & Rammer, 2017). However, climate change can also create negative feedbacks via favouring warm-adapted broadleaved species and reducing the proportion of host tree species of bark beetles (Temperli, Bugmann, & Elkin, 2013; Thom, Rammer, Dirnböck, et al., 2017; Thom, Rammer, & Seidl, 2017b).

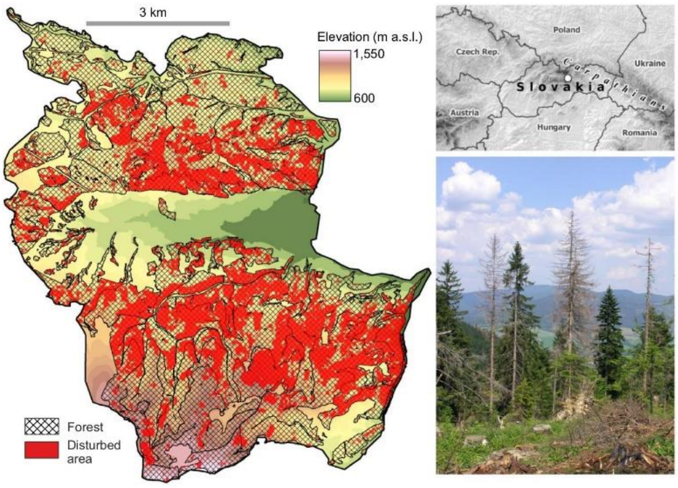
Here we used the individual-based forest landscape and disturbance model iLand (Seidl, Rammer, Scheller, & Spies, 2012) to investigate how different salvaging intensities of windfelled trees affect bark beetle disturbances, and to quantify disturbance impacts on landscape-scale C storage. We specifically addressed the trade-offs between C removal by salvaging and C increases by mitigated bark beetle disturbances, asking whether there is an optimal salvaging intensity balancing the positive and negative effects on forest C storage. Finally, we investigated how climate change—affecting both forest growth and disturbance regimes—impacts ecosystem C storage, and whether the effect of salvage logging is modulated by changing climatic conditions. We focused our analyses on a managed temperate forest landscape in Central Europe which has experienced severe wind and bark beetle disturbances followed by intensive salvaging operations in recent years.

2 | MATERIALS AND METHODS

2.1 | Study region

The Goat Backs Mts. study region is located in central-eastern Slovakia (Lon 20.088–20.275, Lat 48.920–49.061) and covers an area of 16 050 ha (Figure 1). The forest cover is 70% and is dominated

FIGURE 1 Map of the study region and its location in Central Europe. Forest area and the extent of the recent wind and bark beetle disturbance episode (2007–2016) were derived from Landsat satellite imagery. The inset photograph illustrates the situation on site, showing recently bark beetle killed trees (background) as well as indications of recent salvage harvesting (stumps in the foreground)



by Norway spruce (*Picea abies* (L.) Karst.), which makes up 75% of the forest area. The remaining species are European larch (*Larix decidua* Mill.; 10%), Scots pine (*Pinus sylvestris* L.; 9%), Silver fir (*Abies alba* Mill.; 3%) and European beech (*Fagus sylvatica* L.; 2%). The elevation range is 620–1550 m a. s. l. The annual mean air temperature during the growing season (April–September) in the period 1996–2016 was 12°C, and growing-season precipitation was 692 mm. Cambisols and Podsols prevail, whereas Rendzinas occur on calcareous bedrock, which forms the bedrock in the highest reaches of the landscape.

The study region is owned by the church and is under the stewardship of a private forest management enterprise. An even-aged management system with a rotation period of approximately 100 years is applied throughout the landscape. The dominant silvicultural approach to tree regeneration in stands with fir and/or beech admixtures is a uniform shelterwood cut. In the dominant Norway spruce monocultures, a clearcut system is applied. Maximum cutblock size is 3.0 ha in all systems.

The landscape and its recent disturbance history is typical for many Central European forests, and is characterized by severe large-scale disturbances in recent years (Senf et al., 2018). Specifically, the study region has experienced intensive wind and bark beetle (mainly *Ips typographus* L.) disturbances from 2007 onward, which affected as much as 39% of the regional forests (Dobor et al., 2018). The landscape level growing stock decreased from 4.22 Mill. m^3 in 1996 (average of 380 m^3/ha) to 1.93 Mill. m^3 in 2016 (average of 173 m^3/ha). At the same time, the landscape-level forest age distribution was substantially shifted towards an overabundance of young stands (Source: forest management plans [FMP]; National Forest Centre, Slovakia). The main management response to this recent disturbance episode has been a high level of salvage logging, and a reduction in planned harvests. Salvage logging was generally applied with high intensity, although a portion of the disturbed trees remained on site for more than one season for logistical reasons. Mass use of pheromone traps was another measure applied to monitor and reduce bark beetle populations.

2.2 | Simulation model

We used the individual-based forest landscape and disturbance model iLand (Seidl, Rammer, et al., 2012) to dynamically simulate wind and bark beetle disturbance in the study landscape, and evaluate the response of the forest C cycle to various salvaging intensities under climate change. The main entities simulated in iLand are trees, for which the demographic processes of growth, mortality and regeneration are simulated. Processes at the stand and landscape-scale constrain the dynamics of individual trees, and large-scale patterns emerge from tree-level interactions (Seidl, Rammer, et al., 2012).

Trees are simulated as adaptive agents that compete for resources (light, water and nutrients) (Seidl, Rammer, et al., 2012). Production physiology is modelled in a simplified process-based manner using a light use efficiency approach (Landsberg & Waring, 1997). Species-specific environmental modifiers are applied to account for the effect of environment on the total intercepted radiation (APAR), which drives gross primary production (GPP). Temperature, soil water availability, vapour pressure deficit, soil nitrogen availability and atmospheric CO_2 are considered influences on GPP. APAR further depends on tree leaf area, tree position in the canopy and radiation use strategy (light-demanding or shade-tolerant). Individual tree mortality is simulated based on species-specific maximum size and age as well as the occurrence of stress (Seidl, Rammer, et al., 2012). C starvation is used as a process-oriented indicator of tree stress, and can result from competition for resources as well as suboptimal environmental conditions for tree growth (e.g. drought). The model simulates live C stocks in stem, branch, foliage, coarse root and fine root compartments. Snags and the transition from snags to downed woody debris are considered explicitly. A closed C cycle is simulated by also tracking the fate of C in detritus and soil pools (Thom, Rammer, Dirnböck, et al., 2017; Thom, Rammer, & Seidl, 2017b).

iLand simulates disturbances in a spatially explicit manner and currently contains process-based modules for wind (Seidl, Rammer, & Blennow, 2014), bark beetle (Seidl & Rammer, 2017) and fire disturbances (Seidl, Rammer, & Spies, 2014). Wind disturbances are simulated based on wind data such as peak wind speed, wind direction and storm duration. The model initiates wind disturbance in locations where canopy rugosity changes abruptly, that is where vertical differences between the top heights of neighbouring grid cells exceed 10 m (e.g. Blennow & Sallnäs, 2004). Wind speed at the canopy top height is calculated based on a vertical wind profile at the stand edge. Wind data and individual tree turning coefficients are used to calculate critical wind speeds for uprooting and tree breakage based on the approach of Gardiner, Peltola, and Kellomäki (2000). The effect of a given wind event is simulated iteratively, with forest structure (including the appearance of new edges) being updated after each iteration (horizontal resolution: 10 m grid cells). Simulated wind disturbances thus emerge dynamically from the interplay of landscape structure and configuration with a given wind event.

With regard to bark beetle disturbances iLand considers bark beetle phenology and development, the spatially explicit dispersal of beetles, host tree colonization and defence, as well as temperature-related overwintering success (Seidl & Rammer, 2017). Host trees are Norway spruce trees with a diameter at breast height (DBH) of >15 cm. An outbreak can be triggered by a wind disturbance simulated by the model, or occurs based on a climate-sensitive background probability. Bark beetle development is simulated based on the climate-sensitive development rates for each development stage (Baier, Pennerstorfer, & Schopf, 2007). The model tracks beetle cohorts rather than individuals. The cohort is defined as the minimum number of beetles needed to colonize a tree. Every brood tree disperses a number of beetle cohorts determined by the reproductive rate of the beetle, estimated to range between 4 and 24 (Wermelinger & Seifert, 1999). The dispersal of beetles is simulated in a two-stage approach: First, a symmetrical dispersal kernel is used to calculate the approximate flight distance. Second, beetles actively search for suitable host trees in the local neighbourhood determined via the dispersal kernel (Kautz, Schopf, & Imron, 2014). In this search, wind-disturbed trees are being preferred over healthy trees. For healthy trees, attacking beetle cohorts need to overcome a tree's defence system, which is approximated by its non-structural carbohydrate reserves. Trees can be attacked by multiple waves of beetles per year if the climate allows for the development of more than one beetle generation.

The model was extensively tested across a range of ecosystems in Europe and North America in previous studies (Seidl, Spies, et al., 2012; Silva Pedro, Rammer, & Seidl, 2015; Thom, Rammer, Dirnböck, et al., 2017). Extensive testing of productivity, natural mortality and regeneration patterns for the Goat Back Mts. study landscape was conducted by Dobor et al. (2018). All tests showed satisfactory performance of the model in this study region (see also Appendix S1).

2.3 | Landscape initialization and climatic drivers

We initialized the landscape based on data from FMP provided by the National Forest Centre of Slovakia. The data are collected in the field in 10-year cycles and are recorded for forest stands, which are polygons with a variable size seamlessly covering the total forest area of the landscape. The attributes used to initialize the landscape were tree species, number of trees per hectare, stand age and DBH. Individual tree diameters were randomly drawn from diameter distributions centred on the mean DBH of each stand, and tree height (H) was estimated based on the regional DBH:H functions. Trees below 4 m height were initialized as height cohort (with representative individuals describing groups of similar-sized trees) based on stand-level information derived from FMP.

Soil depth and nitrogen information required to run iLand were derived on a 100 × 100 m grid from the national forest soil database (National Forest Centre). Daily meteorological data from the nearby meteorological station were used for deriving the climate time series driving the simulations (see Dobor et al., 2018 for details). Regional climate model (RCM) simulations conducted in the framework of the CORDEX project (Giorgi, Jones, & Asrar, 2009) were used to evaluate the effect of climate change. Six GCM-RCM combinations driven by two Representative Concentration Pathway (RCP) scenarios (RCP4.5 and RCP8.5) were used. More details on used climate change scenarios can be found in Appendix S2.

2.4 | Experimental design

Simulations were run for the period 1997–2100, assuming a continuation of current forest management. The simulated management operations included planting, tending, thinning and harvesting, with timing and intensity of operations modelled after the management practice currently applied in the region (see Dobor et al., 2018 for more details). The incidence of disturbances and subsequent salvage logging supersede regular management operations, resetting the default stand treatment program.

Seven different salvaging intensity scenarios were tested, corresponding to 0, 20, 40, 60, 80, 95 and 100% of trees salvaged. Both trees killed by wind and bark beetles were salvaged in the year of disturbance. No preventive removal of live trees aiming to halt the spread of bark beetles (sanitation logging) was performed. Most model parameters driving bark beetle dynamics were kept default as reported in Seidl and Rammer (2017) (see Appendix S3 for the parameter values used).

As the projection of extreme wind events in climate models is still highly uncertain we generated time series of future storm events based on past observations. We assumed five wind events to occur between 1997 and 2100, set at the simulation years 5, 30, 50, 75 and 90. For each of these wind events, we derived wind speeds by drawing from a Gumbel distribution parameterized based on the data observed in the nearby meteorological station (see Appendix S4), and set the wind duration to 90 min. In order to account for the stochasticity in future wind events we generated five future wind scenarios from these distributions. Overall, the simulated average wind damage of 0.9–1.2 m^3 ha^{-1} $year^{-1}$ (range of five simulated wind scenarios) corresponds well with the average wind disturbance rate of 0.88 m^3 ha^{-1} $year^{-1}$ (inter-annual range 0.35–2.56 m^3 ha^{-1} $year^{-1}$) reported for Slovakia for the period 1990–2015 (Konôpka, Zach, & Kulfan, 2016). The total number of simulations conducted was 455, consisting of 7 salvaging intensities × 5 wind scenarios × 13 climate scenarios (2 × RCPs × 6 models + reference climate).

Using this simulation framework, we evaluated the effect of salvage logging on total and live landscape C, amounts of C in trees affected by wind and bark beetle disturbance, and the interactions between these variables.

3 | RESULTS

3.1 | Salvaging effects on bark beetle disturbance

In all simulations, the amount of C in Norway spruce trees killed by bark beetles was strongly affected by salvaging intensity (Figure 2a). The complete removal of windblown and bark beetle killed trees (SI 100%) prevented bark beetle outbreaks, and the amount of C in killed spruce trees was low under reference climate in this salvaging scenario (see also Appendix S5). Climate change increased bark beetle disturbances even under a complete removal of windblown trees, and beetles were able to kill 0.2–0.4 tC ha^{-1} $year^{-1}$ (average over the simulation period, including non-outbreak years).

The amount of live tree C affected by bark beetles increased strongly nonlinearly with decreasing salvaging intensity. The retention of only a minor amount of windblown trees (salvaging intensity 95%, which resulted in the retention of 0.07–0.11 tC/ha in dead trees on site; Appendix S6) increased bark beetle disturbances substantially, reaching 0.3 tC ha^{-1} $year^{-1}$ under reference climate (Figure 2). For even lower salvaging intensities (80, 40, 60 and 20%) the annual amount of live tree C affected by bark beetles was in the range 0.4–0.5 tC ha^{-1} $year^{-1}$. These findings indicate that salvaging intensities below 80% have very little effect on bark beetle disturbances.

Climate change increased the amount of live tree C affected by bark beetles two to threefold. Consequently, it also decreased the amount of Norway spruce live tree C (Figure 2b). Climate change also resulted in greater volumes of salvaged C (Appendix S6). While the highest salvaging intensity under reference climate removed 1.2 tC ha^{-1} $year^{-1}$, the removal by salvage harvesting under climate change reached as much as 1.7 tC ha^{-1} $year^{-1}$ (average over the simulation period). The differences between the RCP scenarios were minor, although RCP8.5 simulations showed consistently greater bark beetle influence than those under RCP4.5.

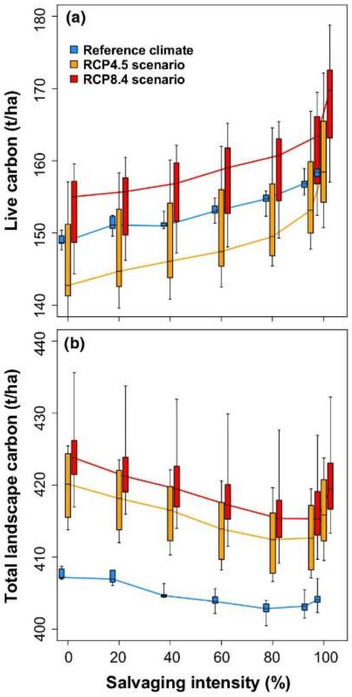


FIGURE 2 The effect of salvage logging intensity (% of disturbed trees removed) on the live tree C affected by bark beetles (tC ha^{-1} $year^{-1}$, a), and the average live tree C stock of Norway spruce on the landscape (tC/ha, b) for different climate scenarios. Each Representative Concentration Pathway (RCP) storyline consists of six different climate model combinations, and each variant was driven by five different wind scenarios. Annual averages over a 104-year simulation period (1997–2100) are presented. Boxes represent the inter-quartile range and whiskers extend to the minimum and maximum values

3.2 | Salvaging effects on landscape carbon

Live tree C on the landscape benefited from salvage logging and increased by 6%, from 149 tC/ha (no salvaging) to 159 tC/ha (100% of disturbed trees salvaged) under reference climate (Figure 3a). The effect of live tree C saved by salvaging was even more pronounced under climate change, and was 8% under both RCP scenarios. The overall climate response of C_{live} regardless of salvaging intensity was variable, with RCP8.5 resulting in increased and RCP4.5 in decreased live tree C compared to the reference climate.

In contrast, total ecosystem C decreased with increasing salvage intensity. Consequently, the effect of C removal via salvaging was stronger than the dampening effect of salvaging on bark beetle disturbances (Figure 3b). At very high salvaging intensities (i.e. >95%), however, C_{total} increased again, with strongly reduced mortality

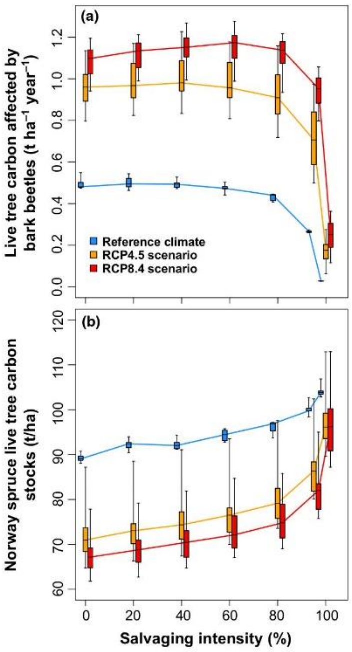


FIGURE 3 Response of live tree carbon (a) and total ecosystem carbon (b) in the landscape (t/ha) to different salvaging intensities under different climate scenarios. Each RCP storyline consists of six different climate model combinations, and each variant was driven by five different wind scenarios. The values are averages over a 104-year simulation period

compensating for losses from timber extraction. The strongest negative effects of salvaging on C_{total} were thus for SIs of 80%–95%, while the difference between SIs of 0 and 100% were minor (between 408 and 404 tC/ha). The effect of climate change on C_{total} was positive, with total ecosystem C storage increasing by 3% and 3.5% under RCP4.5 and RCP8.5 respectively (from 405 to 416 and 419 tC/ha).

3.3 | Interactions between wind and bark beetle disturbances

Higher salvaging intensities resulted in higher levels of live tree C affected by wind disturbance (Figure 4a). This effect was minor under reference climate but was substantial under climate change. Climate change generally decreased the amount of live tree C affected by wind disturbance by 0.18–0.23 tC ha^{-1} year^{-1} for SIs up to 80%, with lower effects under higher SIs.

A considerable trade-off was evident also between wind and bark beetle disturbances. Live tree C affected by bark beetles was negatively correlated with live tree C affected by wind (Figure 4b). The increase in bark beetle disturbances in response to climate change (from 0.38 to 0.89 tC ha^{-1} year^{-1}; see also Figure 2) substantially decreased wind disturbance (from 0.89 to 0.73 tC ha^{-1} year^{-1}). This indicates that the efforts to reduce bark beetle disturbance by salvaging can—in part—be compromised by an increased forest susceptibility to wind. However, an increased impact of bark beetles due to climate change may result in a concomitant decrease in wind impact.

4 | DISCUSSION

Salvage logging is the most frequent management response to forest disturbances world-wide, but its effects on forest ecosystems remain incompletely understood. In the forests of Central Europe salvaging has been applied at unprecedented rates in recent years in response to increasing natural disturbances. In these systems, salvaging of windfelled trees is *inter alia* practiced to reduce the availability of breeding substrate for bark beetles, yet the efficacy of the measure in influencing bark beetle dynamics remains poorly documented. We here quantified the influence of salvaging on subsequent bark beetle dynamics, and estimated the landscape-scale C storage effect of different levels of salvage logging for a temperate forest landscape in Europe.

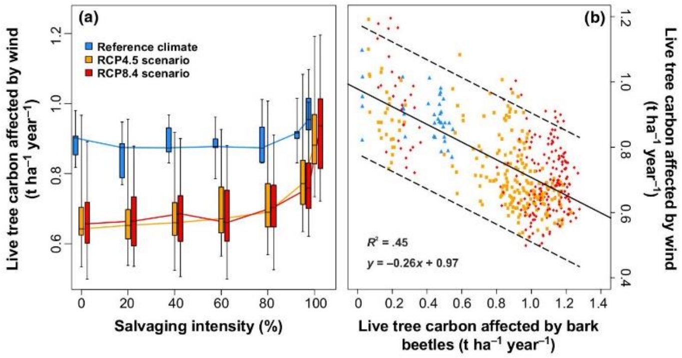


FIGURE 4 The amount of live tree carbon affected by wind disturbance under different salvaging intensities (a) and relationship between live tree C affected by wind and bark beetles (b). The results reached under reference climate and two groups of climate change scenarios (RCP4.5 and RCP8.5) are shown. Linear fit and prediction interval are shown

4.1 | Salvage logging as a means for preventing bark beetle outbreaks

The simulations showed that only the highest salvaging intensities reduced bark beetle disturbance and effectively preserved Norway spruce live tree C. Where the retention of high levels of Norway spruce is of key concern, a very high level of salvage logging is a potent management measure. This finding is consistent with recent management applications of salvaging in Central Europe, aiming to reduce the amount of breeding substrate for bark beetles and thus reducing subsequent bark beetle disturbances (Hlásny & Turčáni, 2013; Økland et al., 2016). However, positive salvaging effects sharply decreased for salvaging intensities of <95%, indicating that even retaining a small amount of wind-felled spruce trees is sufficient for the beetle to make the critical transition from endemic to epidemic population dynamics (Kausrud et al., 2012). Yet, reaching the high salvaging intensities required for positive salvage effects may not be feasible in forest management, particularly when windthrown areas are large and scattered. In contrast to current practice this insight suggests that the removal of windfelled trees with the intention to prevent bark beetle outbreaks should only be applied when such a removal can be achieved with a very high intensity (e.g. when windfelled areas are small and accessible). It is important to note, however, that we here did not analyse the ability of salvage logging to prevent a particular disturbance from spreading, but rather focused on the long-term effects over time frames of typical rotation periods. Moreover, our findings do not address other motivations for salvage logging, such as the recuperation of economic losses or the protection of infrastructure from falling trees (Leverkus, Lindenmayer, et al., 2018; Molinas-Gonzáles et al., 2017).

Climate change is amplifying bark beetle disturbance (Cudmore et al., 2010; Seidl & Rammer, 2017) via weakening tree defence, increasing insect reproduction and reducing winter mortality of bark beetles (Appendix S7). In our simulations, the amount of live tree C affected by bark beetles increased two- to threefold in response to climate change, which is consistent with, for example expected increases for the European Alps (Seidl, Schelhaas, Lindner, & Lexer, 2009). High-intensity salvage logging reduced the amount of live tree C affected by bark beetles also under climate change. Specifically, our results indicate that if a 100% salvage level could be achieved, climate-induced increases in bark beetle disturbances could be efficiently prevented. For realistic levels of salvaging (i.e. <100%), however, bark beetle disturbances increased strongly in our simulations. This indicates that management responses that were deemed successful in the past, such as salvage logging, are not efficient in preventing a climate-related intensification of disturbance regimes. Measures reducing disturbance risk and increasing forest resilience to disturbance are thus needed (Seidl, 2014). Such measures include silvicultural approaches creating forests that are less prone to the impact of natural disturbances (Seidl, Albrich, Thom, & Rammer, 2018), and that facilitate fast recovery from disturbances once they occur (Johnstone et al., 2016). Specifically, mixed species forests containing both early- and late-seral species and structurally diverse stands with a layer of advanced regeneration in the understorey should be promoted. Retaining biological legacies such as surviving trees and parts of deadwood is another potent means to foster forest resilience to disturbances (e.g. Castro et al., 2011).

4.2 | Effects of salvage logging on landscape carbon

Total landscape C decreased only moderately with increasing salvaging intensities. This weak response underlines the trade-offs between C removed via salvaging and live tree C saved from subsequent disturbances. Similarly, insignificant effects of salvaging on C_{total} were found by Bradford et al. (2012) in a boreal forest disturbed by wind and fire. Moreover, the effects of climate change on total ecosystem C storage were considerably stronger than the effects of salvaging in our simulations, indicating that drivers beyond the influence of forest management might become more important in the future (Seidl et al., 2019). This suggests for management to focus resources on creating disturbance-resilient forests rather than on short-term disturbance prevention.

We here focused on C storage in situ, yet forests also influence the climate via C storage in wood products, the substitution of fossil-based resources as well as changes in forest albedo and latent heat flux (Canadell & Raupach, 2008; Valsta et al., 2017). C in salvaged timber, for instance constitutes a lateral C flux that eventually results in C storage in wood products (e.g. Lamers et al., 2014). As salvage logging potentially influences climate regulation more broadly than analysed here, future work could, for example include the effect of C storage in wood products pools, in order to increase the comprehensiveness of our understanding of salvage logging effects.

In contrast to total ecosystem C, live tree C benefited from salvaging, increasing by between 6% and 8% under highest salvaging intensity. The effect of climate change on C_{live} varied with RCP scenario. A likely reason is the elevated atmospheric CO_2 concentration under RCP8.5, which results in higher C uptake rates in this scenario family. This is in line with the previously reported sensitivity of post-disturbance forest recovery to the increased levels of CO_2 (Dobor et al., 2018). The persistence of a CO_2 fertilization effect, however, remains debated in the literature (Hararuk, Campbell, Antos, & Parish, 2019; Reyer et al., 2014) and is strongly moderated by mycorrhizal associations (Terrer, Vicca, Hungate, Phillips, & Prentice, 2016).

4.3 | Effects of salvage logging on disturbance interactions

Many ecological effects of salvaging are thought to emerge from modified interactions in forest ecosystems (Leverkus, Lindenmayer, et al., 2018). This notion was strongly supported by our quantitative simulation results. Specifically, we observed two types of disturbance interactions being altered by salvage logging—the interaction modification and the interaction chain (Foster, Sato, Lindenmayer, & Barton, 2016).

The direct interaction between wind and bark beetle disturbances in the simulations was mediated by the presence of freshly windfelled trees. Salvaging modified this interaction by reducing the amount of such trees. As expected, this reduction mitigates the impact of bark beetle disturbance. In this regard our findings are well in line with observations (e.g. Økland et al., 2016; Stadelmann et al., 2013). We, however, also found this effect to be strongly nonlinear, with very high salvaging intensities being required in order to achieve this interaction modification.

A more complex and hitherto unrecognized effect emerged from the long-term interaction chain between wind and bark beetles. We found that while high-intensity salvaging can reduce the impacts of bark beetle outbreaks, such a reduction is partly compensated (but not cancelled out) by increased forest susceptibility to wind disturbance. The main mechanism behind this compensation was that mature Norway spruce stands were most susceptible to both wind and bark beetle disturbances (Hlásny & Turčáni, 2013; Wermelinger, 2004). Specifically, the intense suppression of bark beetle disturbances increased the share of dense and mature forests on the landscape, which are subsequently more susceptible to the wind disturbance (Jactel et al., 2009). Wind and bark beetles are thus 'competing' for the most vulnerable stands, and reducing bark beetle outbreaks retains more susceptible stands to be affected by wind.

More broadly, this finding indicates that a strong focus on disturbance prevention may generate overly vulnerable conditions with high levels of C stocks that are susceptible to a diverse set of hazards. In our simulations the reduction of bark beetle disturbances via salvaging led to the opposite effect of the one intended with regard to wind disturbance; a phenomenon known in wildfire management as the *firefighting trap* (Collins, Neufville, Claro, Oliveira, & Pacheco, 2013). Similar reasons have, for example led to a change in the attitude to wildfire management in the USA (Stephens et al., 2013). We suggest that future research should focus on a balanced approach of reducing risks and fostering resilience (Seidl, 2014), rather than aiming to minimize a single risk while inadvertently increasing others.

5 | CONCLUSIONS

Salvaging of trees killed by wind and bark beetles is extensively applied in the coniferous forests of Europe. Our simulations indicate that if the aim of salvage harvesting is to dampen future bark beetle disturbances and conserve live tree C, very high salvaging intensities (i.e. >95% of disturbed trees detected and removed) need to be applied. The application of salvage harvesting is primarily recommended for small and concentrated disturbances where very high salvaging intensities are feasible in practice. Furthermore, our results highlight unexpected compensatory effects, such as increased wind disturbances in response to reduced bark beetle disturbances. We thus conclude that novel management responses to changing forest disturbance regimes are needed, going beyond disturbance prevention and focusing on disturbance resilience.

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AUTHORS' CONTRIBUTIONS

L.D. and W.R. conducted all simulations and data analyses, T.H. and R.S. conceived the ideas and led the writing of the manuscript, I.B. and S.Z. collected the data. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Results are archived in Zenodo open-access repository, https://doi.org/10.5281/zenodo.3244166 (Dobor et al., 2019). Additional information on the used ecosystem model can be found at http://iland.boku.ac.at.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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5.3 Spatial configuration matters when removing windfelled trees to manage bark beetle disturbances in Central European forest landscapes.

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Research article

Spatial configuration matters when removing windfelled trees to manage bark beetle disturbances in Central European forest landscapes

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ABSTRACT

Windfelled Norway spruce (*Picea abies*) trees play a crucial role in triggering large-scale outbreaks of the European spruce bark beetle *Ips typographus*. Outbreak management therefore strives to remove windfelled trees to reduce the risk of outbreaks, a measure referred to as sanitation logging (SL). Although this practice has been traditionally applied, its efficiency in preventing outbreaks remains poorly understood. We used the landscape simulation model iLand to investigate the effects of different spatial configurations and intensities of SL of windfelled trees on the subsequent disturbance by bark beetles. We studied differences between SL applied evenly across the landscape, focused on the vicinity of roads (scenario of limited logging resources) and concentrated in a contiguous block (scenario of spatially diversified management objectives). We focused on a 16 050 ha forest landscape in Central Europe. The removal of >80% of all windfelled trees is required to substantially reduce bark beetle disturbances. Focusing SL on the vicinity of roads created a "fire break effect" on bark beetle spread, and was moderately efficient in reducing landscape-scale bark beetle disturbance. Block treatments substantially reduced outbreaks in treated areas. Leaving parts of the landscape untreated (e.g., conservation areas) had no significant amplifying effect on outbreaks in managed areas. Climate change increased bark beetle disturbances and reduced the effect of SL. Our results suggest that past outbreak management methods will not be sufficient to counteract climate-mediated increases in bark beetle disturbance.

1. Introduction

Disturbances from bark beetles have increased sevenfold in Europe's forests since the 1970s (Seidl et al., 2014a). Recent bark beetle outbreaks have reached supranational scales (Senf and Seidl, 2018), increasingly challenging the management responses traditionally applied to mitigate bark beetle outbreaks. Research indicates that future climate change will further fuel bark beetle outbreaks (Jönsson et al., 2009; Seidl et al., 2017), with potential adverse effects on the sustainable supply of ecosystem services to society (Morris et al., 2018). In particular, the number of generation cycles completed per year will increase for important bark beetle species (Baier et al., 2007; Berec et al., 2013; Fleischer et al., 2016), fanning population growth. Bark beetles can also expand into new territories because of relaxed thermal limitations (Jönsson et al., 2009). In addition, drought events, which are expected to become more frequent in the future (IPCC, 2014; King and Karoly, 2017), reduce the capacity of trees to defend themselves against bark beetle attacks (Matthews et al., 2018).

Taken together, bark beetle disturbances are expected to be among the most climate sensitive processes in forest ecosystems (Lindner et al., 2010). Managing bark beetle outbreaks is thus a key challenge for forest managers. Yet, there are indications that some traditionally applied bark beetle management measures may become inefficient under the conditions expected for the future (Dobor et al., 2019a; Hlásny et al., 2019), making a quantitative evaluation of bark beetle management measures a key priority for research (Morris et al., 2017).

Sanitation logging (SL) has been an important part of the management response to outbreaks of the European spruce bark beetle *Ips*

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typographus (Coleoptera: Curculionidae, Scolytinae) in Europe (Hlásny and Turčáni, 2013; Stadelmann et al., 2013; Wermelinger, 2004). SL entails the removal of infested host trees and/or healthy trees in the vicinity of beetle spots with the aim to prevent and mitigate the spread of bark beetle outbreaks. SL is applied during outbreaks to eradicate infestation spots, from which beetles spread to surrounding stands. It is, however, also applied in endemic phases of bark beetle development (i.e. when populations are low and beetles selectively infest and kill only freshly dead and weakened trees) in order to keep beetle populations below the eruptive threshold (Raffa et al., 2008; Wermelinger, 2004). SL is also used to disrupt the connectedness of outbreak areas via the removal of potential host trees in the vicinity of outbreak spots with the aim to reduce beetle spread (Seidl et al., 2016b).

Outbreaks of the European spruce bark beetle are typically triggered by windthrows (Mezei et al., 2017; Økland et al., 2016; Schroeder and Lindelöw, 2002), which provide large amounts of breeding substrate in form of broken or uprooted trees. As these trees provide favourable breeding conditions but are only weakly protected by tree defences they are preferred by beetles over vigorous live trees (Komonen et al., 2011; Matthews et al., 2018). Large windthrows thus attract beetles from surrounding areas and initially act as a sink for the beetle population. When this resource is exhausted (typically in one to two years), a substantially enlarged beetle population leaves the windthrown area and colonizes surrounding live trees (Eriksson et al., 2007; Wichmann and Ravn, 2001). SL therefore aims to remove windfelled trees before the beetles are spreading to surrounding areas (Schroeder, 2007; Stadelmann et al., 2013; Wichmann and Ravn, 2001).

Despite the long tradition in applying SL in forestry practice there is very little quantitative evidence on the effect of such management measures on bark beetle populations and the amount of trees killed by bark beetles (but see for example Mezei et al., 2017; Stadelmann et al., 2013). This is particularly true for conditions where outbreak areas are large and beetle pressure is high, as is expected for the coming decades. Studies on bark beetle management have instead focused on the assessment and optimization of different trapping devices (Galko et al., 2016; Holuša et al., 2017), have improved the detection of infested trees using remote sensing (Abdullah et al., 2019, 2018), and made recommendations on how to prioritize fellings based on forest structure, storm gap size and other factors (Schroeder, 2010). The broader implications of the removal of disturbed trees has come into focus recently, with assessments of its effects on biodiversity, ecosystem services, forest recovery, as well as carbon and nutrient cycles (Leverkus et al., 2018; Lindenmayer and Noss, 2006; Thorn et al., 2017). The efficiency of SL to reduce subsequent bark beetle damage – frequently given as the primary motivation to conduct SL by managers and thus a key element in the discussion on salvage and SL – remains understudied to date. As SL is time- and labour-intensive, particular questions of interest relate to the optimal rate and spatial pattern of SL, and whether SL will be able to mitigate bark beetle outbreaks under future climatic conditions.

Our overall objective was to evaluate the effect of a wide range of SL intensities and spatial configurations on future bark beetle disturbances. Specifically, we assessed how different spatial configurations of SL on the landscape affect its efficiency for reducing bark beetle disturbances. This question was motivated by the fact that timely SL operations are frequently restricted, either by limited accessibility of disturbed stands (Lamers et al., 2014) or by the nature conservation status of certain tracts of a forest landscape (Müller et al., 2018). Furthermore, we asked if and how climate change modulates the effects of SL treatments on bark beetle dynamics. Based on previous findings and current process understanding we hypothesized that spatially concentrated applications of SL with high treatment intensity are most efficient (Dobor et al., 2019a; 2019b), but that a climate-mediated increase in bark beetle population levels will strongly reduce the efficiency of SL. In order to capture the complex interplay between (future) climate, bark beetle populations, and host trees we employed process-based simulations using the model iLand (Seidl et al., 2012a). Simulation modelling allowed us to overcome common difficulties in the analysis of forest disturbances, such as the quantification of reference conditions (here: a landscape not treated with SL but otherwise similar to the treated landscape).

2. Materials and methods

2.1. Study landscape

The study landscape is located in Slovakia in the Low Tatras Mountains (Central Europe). The landscape covers an area of 16 050 ha, of which 70% are covered with forests. The elevation range is 620–1550 m a.s.l. Air temperature during the growing season (April–September) ranges from 12 to 15 °C, and growing-season precipitation ranges from 380 to 510 mm. Norway spruce (*Picea abies* (L.) Karst.) makes up 70% of the tree species composition, with Silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) as other canopy-dominant tree species. Forests in the region are intensively managed for timber production. The dominant silvicultural approach to regenerate mixed stands containing a fir and/or beech component is a uniform shelterwood cut (a progressive cutting that leads to the establishment of a new cohort of trees under the canopy of the retained mature trees). In spruce monocultures, a small-scale clear-cutting system is applied. The forests in the study landscape have experienced severe wind and bark beetle disturbances since 2007, affecting 39% of the forest area until 2010 (Dobor et al., 2018). Management responses to disturbance include extensive salvage and SL, beetle trapping, a decrease in regular harvests as well as efforts to establish stands with a more diverse tree species composition in order to decrease future disturbance risk. The disturbance patterns and management responses in our study landscape are characteristic for the recent disturbance history in many Central European forest landscapes (Senf et al., 2017).

2.2. Definitions

There is considerable terminological confusion in the literature regarding management measures applied to mitigate bark beetle outbreaks. The term sanitation logging is often used interchangeably with the term salvage logging (e.g. Fettig et al., 2007). In other instances, the two terms are used to denote different aspects of bark beetle management (e.g. removal of windblown trees to prevent their infestation vs. removal of standing infested trees to prevent beetle spread; Stadelmann et al., 2013; Wermelinger, 2004). We here define sanitation logging as any tree removal activity which aims to prevent the risk of bark beetle attack to adjacent trees and/or mitigate bark beetle spread. In contrast, we use term salvage logging for tree removal activities which are conducted with the primary aim to recoup economic losses from disturbances or reduce disturbance-induced hazards to infrastructure and human safety (Molinas-Gonzáles et al., 2017).

2.3. Simulation model

The model iLand (Seidl et al., 2012a) is a process-based ecosystem model that simulates forest landscape dynamics in a hierarchical multi-scale framework (e.g., Mäkelä, 2003), i.e. treating different processes at different spatial and temporal scales. The main entity in the model is a tree, for which the demographic processes of growth, mortality, and regeneration are simulated. Processes at the stand and landscape scale constrain the dynamics of individual trees and thus allow for a robust scaling of tree-scale processes to large areas (Seidl et al., 2012a). The model was extensively tested and evaluated across a range of ecosystems in Europe and North America in previous studies (Braziunas et al., 2018; Seidl et al., 2012b; Silva Pedro et al., 2015; Thom et al., 2017a). Furthermore, the model was successfully tested for the study landscape investigated here by Dobor et al. (2018), focusing on productivity, natural mortality (i.e. mortality caused by stress and competition for resources) and regeneration patterns in a pattern-oriented modelling approach.

iLand simulates disturbances in a spatially explicit manner and contains process-based modules for several disturbance agents. Wind disturbance is simulated in the model based on input regarding wind (i.e., speed, direction, duration, day of year of occurrence), which can be derived from meteorological observations of specific wind events, statistical descriptions of historical wind regimes, or simulations generated by climate models (Seidl et al., 2014a). The model initiates wind disturbances in locations, where canopy rugosity changes abruptly, i.e., where vertical differences between the top heights of neighbouring grid cells exceed 10 m (e.g. Blennow and Sallnäs, 2004). The impact of a wind event is simulated iteratively, with forest structure – including the appearance of new edges – being updated over the course of the duration of the wind event. In each iteration the model calculates critical wind speeds for uprooting and breakage of affected trees (Seidl et al., 2014a) if the wind speed in the current iteration exceeds these critical wind speeds, the tree is either broken or uprooted. The simulated wind disturbance patterns are thus an emergent property of the wind forcing in combination with the prevailing forest structure.

The iLand bark beetle disturbance module simulates phenology and development of the European spruce bark beetle, spatially explicit dispersal of beetles, colonization and tree defence, as well as temperature-related overwintering success of beetles (Seidl and Rammer, 2017). Outbreak are either triggered by wind disturbance, or happen independently based on climate-sensitive background infestation probability. Bark beetle development is simulated based on temperature-sensitive beetle phenology (Baier et al., 2007), allowing for the development of multiple beetle generations per year under favourable climatic conditions. For reasons of computational efficiency the model does not track individual beetles but beetle cohorts, which are defined as the minimum number of beetles needed to colonize a tree. Every brood tree disperses a number of beetle cohorts determined by the effective reproductive rate of the beetles, which was here set to 20 (see Wermelinger and Seifert, 1998). Sister broods are assumed to have a 50% reduced reproductive rate (Anderbrant, 2006). The emerging beetles disperse in two stages: First, their general dispersal distance and direction is determined based on a symmetrical dispersal kernel parameterized from field data. Subsequently, beetles actively search for host trees within their perceptive range. A beetle cohort attacking a tree has to first overcome the trees' defence system. iLand dynamically simulates tree stress based on the carbon balance of a tree. The thus derived stress index is used as an indicator of tree defence against bark beetles. Freshly wind-disturbed trees are assumed to be defenceless against bark beetle attacks, and are thus also preferred by beetles in their host search. Consequently, the timely removal of windfelled trees (i.e., before beetle development is completed) affects the subsequent bark beetle outbreak dynamics. Simulated natural bark beetle mortality accounts for both overwintering mortality and density-dependent effects of antagonists.

2.4. Landscape initialization and experimental design

Data from Forest Management Plans (FMP; Source: National Forest Centre, Slovakia) were used to initialize the current state of the forest vegetation in the simulations. The data were collected in the field at a 10-year inventory cycle, and contain statistical descriptions of forest stands within compartments with variable size (ca 3–15 ha). The FMP attributes used to initialize the landscape in iLand were number of trees per hectare, stand age, and diameter at breast height (DBH). Individual tree diameters were randomly drawn from diameter distributions centred on the mean DBH of each stand, with the variance derived from forest plots in the region. Tree heights of all individuals were calculated based on species-specific diameter-height curves. Saplings (trees below 4 m height) were initialized as height cohort with tree height data derived from FMPs. iLand furthermore requires information on soil type and depth and uses plant-available nitrogen (N) as a proxy for nutrient availability. This information was derived from the national forest soil database of Slovakia (Source: National Forest Centre, Slovakia).

We evaluated forest development under different intensities and spatial patterns of SL for the period from 1996 (i.e., the year of the initialization of the study landscape based on FMP data) to 2050. We used this time horizon because of its relevance for current management decision making. Moreover, climate conditions after 2050 start to critically constrain spruce persistence in our study landscape. Reference climate data (i.e. representing a continuation of past climatic conditions) were developed based on the observed climate for 1996–2016 by random sampling of years with replacement. To assess the effects of climate change, we studied six climate change scenarios, derived from three regional climate model (RCM) runs conducted within the framework of the CORDEX project (Coordinated Regional Climate Downscaling Experiment; Giorgi et al., 2009). Each RCM was driven by two Representative Concentration *Pathway scenarios*, i.e., RCP 4.5 and RCP 8.5 (Supplementary material).

We prescribed wind events to occur in the years 2000, 2010 and 2030 in all scenarios. Each wind event was simulated with five different wind speeds, which were randomly drawn from a distribution of maximum hourly wind speeds observed at the nearby meteorological station Poprad–Gánovce (Source: Slovak Hydrometeorological Institute) between 1996 and 2018. The simulated wind events were 90 min long, and wind directions were set based on the prevailing wind directions in the region (east-northeast in 2000, west-southwest in 2010 and 2030). The average amount of windfelled trees simulated with these settings corresponded well with observed wind disturbance data for Slovakia between 1990 and 2015 (Konôpka et al., 2016).

Bark beetle dynamics was simulated based on the model structure and parameterization introduced by Seidl and Rammer (2017) (see also Supplementary material). Simulated bark beetle disturbances matched observed bark beetle dynamics well, with the proportion of bark beetle disturbed timber volume being in the range of 70–120% of windfelled timber (based on national forest damage statistics, Source: National Forest Centre, Slovakia) and with bark beetle infestations occurring primarily in the vicinity of windthrows with only minor infestation spots occurring independently of windthrows (based on the inspection of satellite imagery from the region; Dobor et al., 2018; Potterf et al., 2019).

To assess the effect of the spatial configuration of SL we simulated three different spatial patterns: uniform SL over the entire study landscape (U), SL only in the vicinity of forest roads (R), and SL in a contiguous subset of the landscape (block design, B) (Fig. 1). Scenario R represents a situation in which limited logging resources are available, restricting sanitation efforts to stands that are easily accessible. In contrast, scenario B illustrates the development if different management objectives need to be met on the landscape, with SL being restricted to

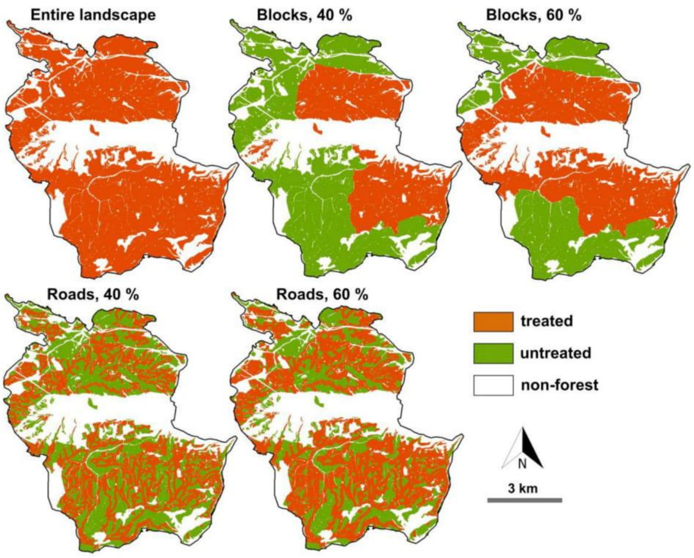

Fig. 1. The five spatial configurations of sanitation logging studied on the landscape. Percent values in the figure indicate the proportion of the total forest area that is treated.

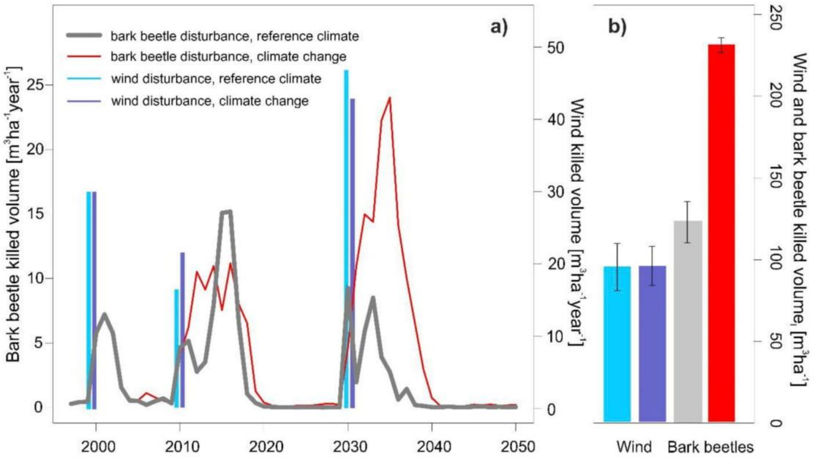

Fig. 2. (a) Temporal development of wind and bark beetle disturbance in Norway spruce stands simulated by iLand in the absence of sanitation logging. Shown is the average over five wind scenarios and an ensemble of climate change scenarios. Columns indicating the wind impact under reference climate and climate change are displayed in different years for presentation purposes. (b) Cumulative timber volume disturbed over the 54-year simulation period under different climate conditions is shown.

certain areas, while other areas are exempt from treatments (e.g., due to considerations of nature conservation). Two treatment levels were simulated for scenarios R and B, treating 40% and 60% of the total forest area in the landscape. These two SL intensities correspond to buffer widths of 60 and 100 m (in each direction from the road), respectively, in the scenario R. For each spatial configuration scenario different levels of SL intensity were simulated, representing different percentages of windfelled trees detected and removed by management. In scenarios R and B, SL intensities of 60% and 95% (I60, I95) were simulated, resulting in a total of eight SL scenarios: R40-I60, R40-I95, R60-I60, R60-I95 and B40–I60, B40–I95, B60–I60, B60–I95. In the uniform scenario U, a total of seven different SL intensity levels forming an intensity gradient were simulated (i.e., 0, 20, 40, 60, 80, and 95% of windfelled trees removed).

The effect of SL was evaluated with regard to three different response variables: (i) the landscape-scale reduction of bark beetle disturbance relative to values reached in the absence of SL, (ii) the disturbance reduction in the treated areas, and (iii) the disturbance reduction in untreated areas. To consistently compare the effects of different spatial configurations and intensities of SL we derived a standardized sanitation intensity (SSI, %), which was calculated as the sanitation intensity (SI, %) multiplied by the portion of treated forest area (Area, %) (Eq. (1)):

$$SSI = \frac{SI \times Area}{100} \qquad [1]$$

In scenario U the SSI equals SI. To further elucidate SSI values, we also investigated the relationship between SSI, the amount of disturbed spruce volume extracted, and the amount of remaining disturbed spruce volume (Appendix A).

3. Results

3.1. Wind and bark beetle impacts in the absence of sanitation logging

The amount of spruce trees disturbed by wind ranged from 25 to 40 m^3 ha^{-1} during the wind event in the year 2000 (range is based on simulation outputs driven by 5 different wind settings), with 11–23 m^3 ha^{-1} and 39–60 m^3 ha^{-1} being disturbed in the years 2010 and 2030, respectively (Fig. 2). This represents 8–14, 3–7 and 12–21% of the Norway spruce growing stock in the landscape. Each wind event triggered outbreak of bark beetles, with 20–26, 51–77 and 30–45 m^3 ha^{-1} killed volume in the absence of SL. The average bark beetle disturbance during the full simulation period was 2.0–2.5 m^3 ha^{-1} $year^{-1}$ ($Dist_{vol}$), representing an annual loss rate of 0.6–0.8% of live spruce volume on the landscape (Dist%) (Appendix B).

Climate change affected the windfelled volume only marginally in the first wind event, while the remaining two windthrows were more sensitive to climate change (Fig. 2). The timber volume affected by bark beetles increased by 1–17, 11–40, and 220–300% in the three outbreak waves under climate change compared to reference climate. $Dist_{vol}$ was in the range of 4.2–4.3 m^3 $ha^{-1}year^{-1}$, resulting in a cumulative timber volume disturbed of 226–234 m^3 ha^{-1} over the 54-year simulation period; the cumulative amount reached under reference climate was 111–136 m^3 ha^{-1}, Fig. 2). Climate change resulted in larger and more severe bark beetle epidemics, while the endemic phases between outbreaks remained similar to reference conditions also under climate change.

3.2. Effect of sanitation logging on bark beetle disturbance

3.2.1. Logging equally across the landscape

The live spruce volume annually affected by bark beetles (Dist%) decreased nonlinearly with increasing SI when the treatment was applied throughout the entire landscape (Fig. 3). A strong decrease in Dist% occurred at SIs above 60%, corresponding to the retention of less than 1.5 m^3 $year^{-1}$ ha^{-1} of disturbed spruce timber on the landscape

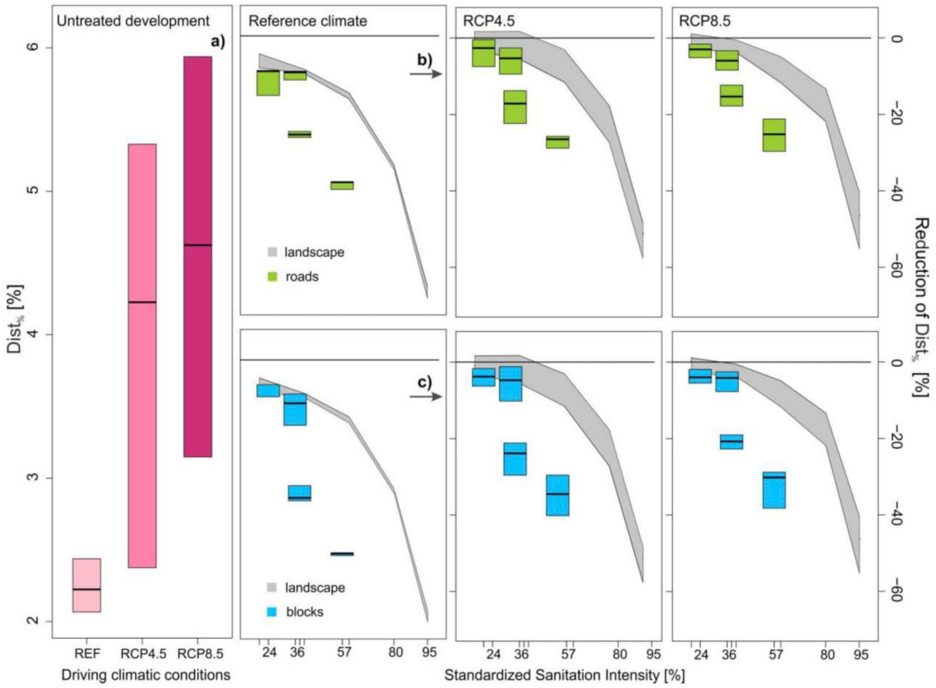

Fig. 3. Response of the per cent of living spruce killed by bark beetles (Dist%) to different intensities of sanitation logging conducted equally over the whole landscape, within road buffers and within contiguous blocks under three different climate conditions. Figure a) shows values of Dist% in the whole landscape without sanitation logging, which is the reference value for figures b) and c). Figures b) and c) show relative differences from values reached under the variant with no sanitation logging. REF - Reference climate, RCP - Representative Concentration Pathway scenario.

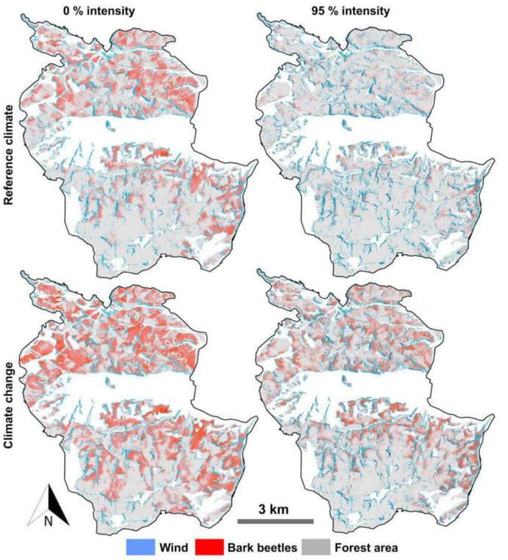

Fig. 4. Spatial distribution of disturbances by wind and bark beetles between 1996 and 2050. Forest stands where total amount of disturbed trees during the 54-year period was above 0.03 m^3 ha^{-1} are highlighted. Variants with and without the effect of sanitation logging of windfelled trees are shown. Each variant was simulated under reference climate and climate change. The maps showing the effect of climate change result from averaged simulation outputs driven by three climate models nested within two greenhouse gas concentration scenarios RCP4.5 and RCP8.5 (i.e. six climate trajectories), and by 5 wind event time series.

(see Appendix A for the relationship between SI and the spruce timber volume retained and extracted). An SI of 80% decreased Dist% by 34% relative to simulations without SL, and an SI of 95% by 67%.

Climate change decreased the efficiency of SL regardless of sanitation intensity. While Dist% increased at least threefold as a result of climate change (Fig. 3), the dampening effect of SL decreased from 67% under reference climate to 47% under climate change for an SI of 95%. For an SI of 80%, the suppressing effect decreased from 34% under reference climate to 17% under climate change.

Spatial pattern of bark beetle disturbance in the absence of SL and with a high intensity sanitation removal can be seen in the maps in Fig. 4.

3.2.2. The effect of different spatial patterns of sanitation logging

We used standardized sanitation intensity (SSI; Eq. (1)) to compare different spatial patterns of SL to the previously described effect of applying sanitation throughout the entire landscape (Fig. 3, Supplementary material). SL of blocks and road buffers on 40 and 60% (R40, B40 and R60, B60) of the landscape with an intensity of 95% (i.e. resulting in a SSI of 38 and 57%, respectively) reduced Dist% more efficiently than applying the same SSI throughout the landscape. This indicates a greater sanitation success if the treatment was conducted with high intensity over a small area compared to removing approximately the same amount of infested trees distributed across the entire landscape. The difference between spatial patterns of SL was, however, not significant for small SSI values. SL was more efficient when applied in blocks than in road buffers. Climate change reduced the efficiency of sanitation regardless of spatial pattern.

3.2.3. Sanitation effects on treated and untreated areas

SL of 60 and 95% intensity applied only within road buffers covering 60% of the total area of landscape decreased the amount of trees killed by bark beetles from 2.23 (variant without SL) to 2.03 and 1.27 m^3 ha^{-1} year^{-1} inside the treated area (i.e. by 9 and 43%, Fig. 5). In case of 95% SI inside the road buffer the damage (1.27 m^3 ha^{-1} year^{-1}) was higher compared to the case when SL was applied over the whole landscape (0.85 m^3 ha^{-1} year^{-1}). For 60% SI the difference is smaller. Specifically, bark beetle disturbances in untreated areas were reduced from 2.24 to 2.17 and 1.91 m^3 ha^{-1} year^{-1} (i.e. by 3 and 15%) through treating road buffers. Hence, SL in road buffers dampened disturbances outside of the treated areas via inhibiting the spread of bark beetles.

Blocked SL (95% intensity) reduced the disturbance rate within the treated areas by 63% (from 2.62 to 0.96 m^3 ha^{-1} year^{-1}), and damage rates did not differ significantly from values reached under the SL applied in the whole landscape (1.00 m^3 ha^{-1} year^{-1}) (Fig. 5). SI of 60% resulted in the reduction of bark beetle disturbance by 11%. Bark beetle disturbances in untreated areas were not affected by blocked SL, with disturbance levels outside treated areas equalling those in simulations without SL. In contrast to SL along roads, the interaction between treated and untreated areas was negligible in the block design.

Climate change reduced the overall efficiency of SL; disturbance reduction with SI of 95% within road buffers was only 21% (compared to 43% under reference climate) and effect on untreated areas was negligible. In case of blocked SL, disturbance reduction was 34% only, compared to 63% under reference climate. Effect of SL with intensity of 60% was negligible in either spatial design (Fig. 5).

Similar effects as were previously described were observed also when only 40% of the landscape was treated (not shown here), though the effect of SL was less distinct.

4. Discussion

4.1. Methodological considerations and limitation

We used a process-based model allowing us to dynamically quantify disturbance impacts, their interactions and feedbacks on vegetation, as well as the effects of climate change and management in a consistent simulation framework. Our approach not only accounted for the amplifying direct effects of climate change on bark beetle development and tree defence capacity but also considered negative vegetation feedbacks such as a modified forest structure and consequently disturbance susceptibility after outbreaks (Thom et al., 2017b), and thus realistically mimics the complexity of the interactions between vegetation dynamics, climate and disturbances.

Despite the high level of process detail of our simulation framework, reproducing complex disturbance regimes in models remains challenging (Seidl et al., 2011). Processes not considered in the model applied here include, for example, the effect of altered microclimate at forest edges that emerge after harvests or windthows on the development of bark beetles (Kausrud et al., 2011; Kautz et al., 2013). It is thus important to test the applied model – being a simplification of reality – with regard to its ability to reproduce patterns observed in reality (Grimm et al., 2005). In this regard we previously conducted in depth analyses on the plausibility of simulated vegetation – disturbance interactions, including regeneration after disturbance and post-disturbance productivity patterns (Dobor et al., 2018; Thom et al., 2017a). The plausibility of simulated wind impacts and bark beetle dynamics was successfully evaluated against independent data (Seidl and Rammer, 2017). Moreover, the used model settings generated a good match of here simulated bark beetle dynamics with observed

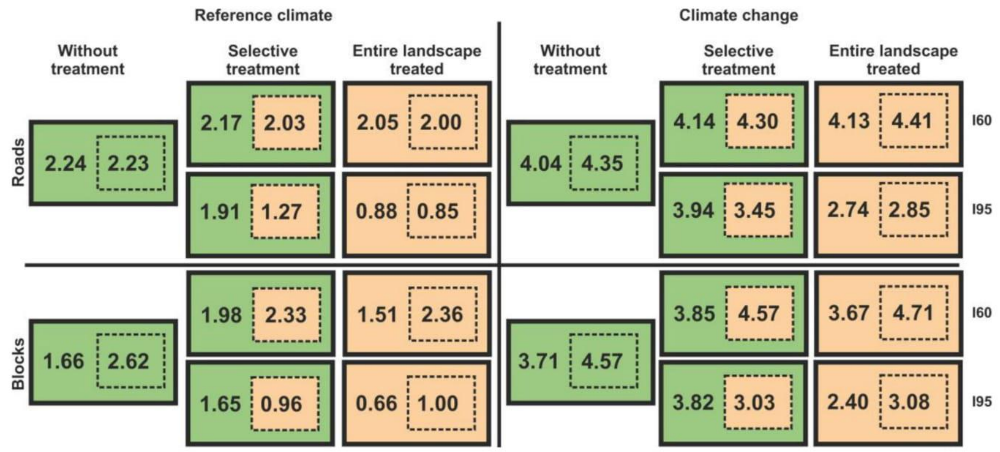

Fig. 5. Effect of different spatial configurations of sanitation logging on bark beetle disturbance. Large rectangles represent the entire landscape, and the embedded rectangles represent areas of blocks and road buffers (green – area without treatment, orange – treated area). The left column (Without treatment) indicates the average volumes of trees killed by bark beetles (m^3 ha^{-1} $year^{-1}$) in the absence of sanitation logging (highest disturbance). The middle column (Selective treatment) shows situation, when only the areas within road buffer or blocks were treated (intermediate disturbance level). The right column (Entire landscape treated) indicates the same values reached with sanitation logging applied equally over the landscape (lowest disturbance). Two intensities of sanitation logging are presented – 60 and 95% (rows). The figure present variant where the treated area covers 60% of the entire landscape (see Methods for details). Simulation outputs for reference climate and average of six climate change scenarios are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

infestation patterns in terms of the proportion between wind and bark beetle damage and the close adjacency of bark beetle infestations to the windfelled stands (e.g. Potterf et al., 2019). An important deviation from expected patterns was observed with regard to the spatial pattern of simulated wind impact, which was relatively scattered throughout the landscape (i.e. occurring at wind-exposed forest edges, based on the model logic). In the Carpathian Mountains, however, wind disturbances are often triggered by strong katabatic winds (also called bora), which frequently result in large high-severity patches of wind disturbance (Fleischer, 2008). Differences in wind disturbance patterns may in turn result in different bark beetle dynamics in the simulations. For example, Potterf and Bone (2017) found that the scattered windthrow is more conducive to bark beetle outbreaks than large, concentrated wind disturbance patches. This underlines that the spatial variation in windthrow patterns and their effect on bark beetle dynamics warrants attention in future research.

Another aspect that needs to be considered in the interpretation of our results is the specific implementation of SL simulated here. Although forest management typically strives to remove the windfelled trees as soon as possible in order to prevent wood degradation and colonization by beetles (Wermelinger, 2004), a swift treatment is often hampered by logistical challenges and considerations of forestry operation. We here exclusively simulated SL removals in the year of disturbance, i.e. before colonizing beetles can spread to surrounding areas. In reality, however, colonization of and dispersal from windfelled trees can happen simultaneously over a period of several years. Studies show, for instance, that the colonization rate of windfelled spruce trees can be higher in the second year than in the first year after the storm (Schroeder, 2010). Some evidence even suggests that windfelled trees are suitable breeding material for bark beetles for more than three summers (Wermelinger et al., 2013), particularly when cold and wet conditions keep the phloem of windfelled trees moist (Holuša et al., 2017). A further management measure in the context of responding to bark beetle outbreaks in Central Europe is the search for and removal of standing infested trees in the surrounding of the windfelled areas or previous infestation spots (Wermelinger et al., 2012). We did not simulate this measure here in order to being able to isolate the effect of removing windfelled trees on bark beetle dynamics. Further works should include this element of SL, as its efficiency remains incompletely understood (e.g. Stadelmann et al., 2013), particularly where outbreak areas are large.

4.2. Implications for outbreak management

Our findings indicate that even relatively small amounts of windfelled Norway spruce trees remaining after high intensity SL are sufficient to trigger a transition from endemic to epidemic conditions in the population dynamics of the European spruce bark beetle. This critical transition was further facilitated by climate change, which amplified the simulated bark beetle disturbance even under very high intensity SL. This finding is supported by the analyses of Marini et al. (2017), who found that bark beetle population eruptions can be driven by climate when the amount of windfelled trees is small. In contrast, a large surplus of windfelled trees can boost population dynamics above the threshold for a successful colonization of healthy trees irrespective of climate conditions. This indicates that outbreaks can be prevented by high intensity SL only under a specific set of factors, i.e. if windblown areas are limited, windfelled trees can be efficiently removed and climate conditions are not particularly favourable for bark beetle development. Due to the climatic changes expected for the coming decades, such constellations will become less likely in the future, and outbreaks will be increasingly triggered even in the absence of windfelled trees (Marini et al., 2017; Netherer et al., 2015; Seidl et al., 2016a). This makes the „hotter droughts" (Millar and Stephenson, 2015) expected for the future a particular concern in the context of forest disturbances (Sommerfeld et al., 2018).

Consistently with previous research (e.g. Jönsson et al., 2009; Seidl et al., 2009), climate change had a strong impact on the simulated future bark beetle disturbance in our analyses, and caused a doubling of the timber volume disturbed by bark beetles. Climate change also reduced the efficiency of SL, with the effect being more pronounced at low intensities of SL. Given that achieving high SL intensities could be increasingly challenged by more frequent and severe disturbances in the future (Seidl et al., 2017), climate change could render SL to become largely inefficient. It is also noteworthy that we here only focused on the first half of the 21st century, in which climate change is still relatively moderate compared to the later parts of the century. Consequently, the efficiency of SL can be expected to decrease even more strongly than reported here in the second half of the 21st century. However, over longer periods of time also dampening feedbacks on bark beetle outbreaks can be expected via changes in forest structure and composition (Temperli et al., 2013; Thom et al., 2017c).

We here tested the effect of different spatial patterns of SL, with important implications for the management of Norway spruce forests in Europe. We first focused on treatments along the existing road network, as accessibility is often a key factor limiting the timely implementation of management measures. Although limited levels of road infrastructure are typical for, for example, Canada or Siberia (Lamers et al., 2014), many European regions also suffer from an insufficiently developed forest road network. This can, for example, lead to overharvesting of accessible locations, limited options for small-scale silvicultural interventions or inefficient disturbance management, including salvage and sanitation operations (Kolström et al., 2011). We found that conducting SL exclusively along roads – even when applied at high intensity – was not effective in reducing bark beetle disturbances, with the landscape-scale rate of disturbance being close to the untreated simulations. This finding is likely related to the width of the road buffers treated here (120 and 200 m, respectively), which was chosen to reflect considerations of forest engineering rather than those of bark beetle ecology. As the effective dispersal range of the European spruce bark beetle is around 500 m (e.g. Kautz et al., 2011; Potterf et al., 2019), considerably wider buffers would be needed to shelter areas from dispersing beetles. Treating road buffers did, however, also dampen bark beetle outbreaks in adjacent untreated areas, as the road network in our study landscape is well developed and treatments along roads create breaks for the spread of the disturbance (similar to fire breaks on the landscape, Russo et al., 2016). Efficiency of SL within road buffers was, however, largely reduced by climate change.

The second spatial pattern of SL analysed here addresses the concerns about bark beetles spreading from non-intervention areas to neighbouring production forests (Grodzki et al., 2006; Montano et al., 2016; Potterf et al., 2019; Potterf and Bone, 2017). In this regard we could show that applying SL in a blocked design (i.e., only in the parts of the landscape designated as intensively managed) substantially reduced the impact of bark beetles on the areas treated and, equalled the efficiency of SL treatments applied across the whole landscape. This indicates that retaining the deadwood created by wind disturbances in some portions of the landscape (e.g., in order to increase biodiversity) does not harm production forestry in other parts of the landscape as long as SL is applied intensively in the latter areas. In contrast to applying SL along road buffers, blocked SL did not dampen outbreaks in adjacent untreated areas. This finding can be partly attributed to the relatively even distribution of wind disturbances in our landscape, which triggered bark beetle outbreaks throughout the simulation area. If wind disturbance risk would be high in treated and low in untreated areas (e.g., due to an elevated structural and compositional diversity of the latter), a stronger influence of treatments on untreated areas could be expected.

5. Conclusions

While the evidence for an ongoing intensification of forest disturbances in Europe is growing (Seidl et al., 2014b; Senf et al., 2018), our current understanding of the efficiency of approaches to dampen disturbances through management remains incomplete. This particularly applies for the management of bark beetles, which are strongly responding to climate change, while their management remains largely based on past heuristics. Here we show that the magnitude of bark beetle disturbances will increase further in the coming decades, while the efficiency of SL of windfelled trees in dampening bark beetle outbreaks declines. We specifically show that due to a climate-mediated proliferation of bark beetle development also a very limited amount of windfelled trees is sufficient for triggering the critical transition from endemic to epidemic population dynamics. Our study further highlights that applying SL at low to medium intensities is not efficient and should thus be avoided. In contrast, early and concentrated removal of windfelled trees can substantially reduce the impact of bark beetles.

Data availability statement

Results are archived in the Zenodo open-access repository, http://doi.org/10.5281/zenodo.3484679 (Dobor et al., 2019b). Additional information on the used ecosystem model, including the source code can be found at http://iland.boku.ac.at.

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Appendix A. Relationship between the intensity of sanitation logging and amounts of extracted and retained spruce trees

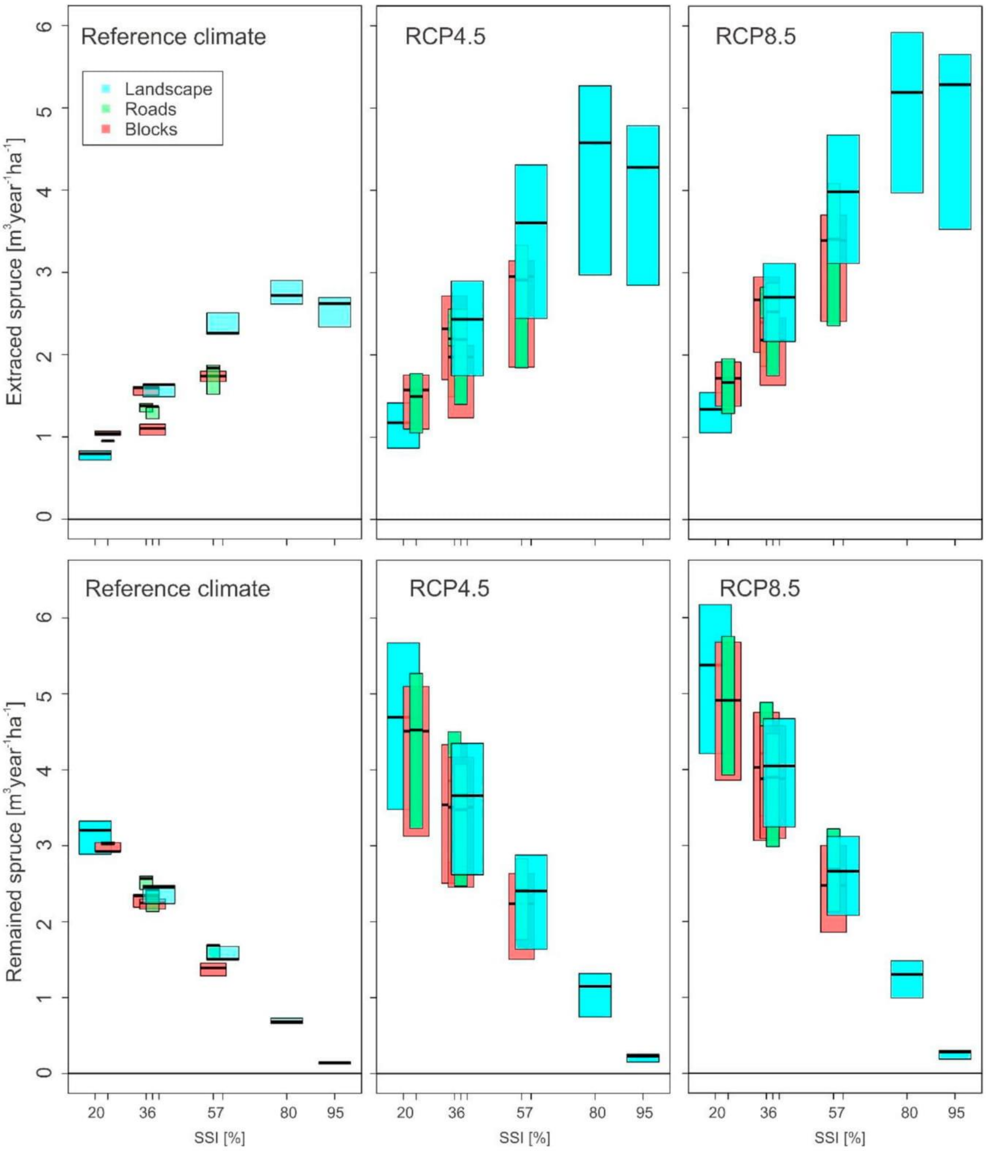

Fig. A1. The average extracted and remained volume of spruce trees affected by wind and bark beetles during the simulation period for different SSI-s under three climate conditions

Appendix B. Selected indicators of simulated forest development affected by wind and bark beetle disturbance

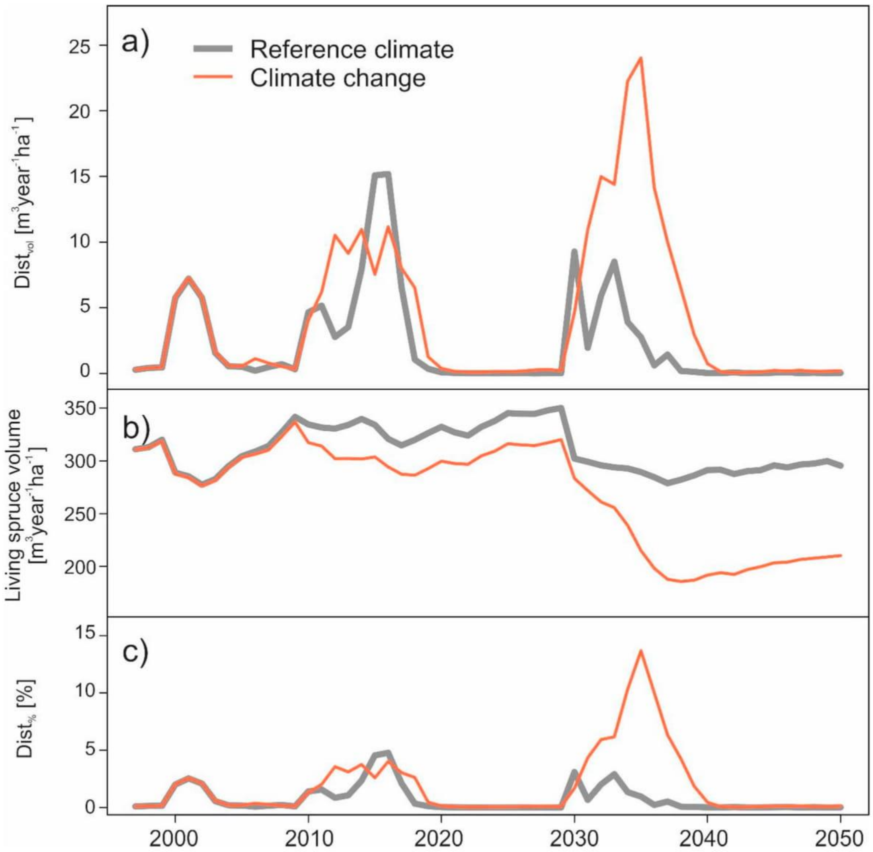

Fig. B1. Wood volume affected by bark beetles (a), volume of live spruce trees (b) and the percentage of bark beetle affected volume (c). Values without sanitation logging are shown.

Appendix. CSupplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2019.109792.

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5.4 Contrasting vulnerability of monospecific and species-diverse forests to wind and bark beetle disturbance: The role of management.

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ORIGINAL RESEARCH

Contrasting vulnerability of monospecific and species-diverse forests to wind and bark beetle disturbance: The role of management

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Abstract

1. Wind and bark beetle disturbances have increased in recent decades, affecting Europe's coniferous forests with particular severity. Management fostering forest diversity and resilience is deemed to effectively mitigate disturbance impacts, yet its efficiency and interaction with other disturbance management measures remain unclear.
2. We focused on Central Europe, which has become one of the hotspots of recent disturbance changes. We used the iLand ecosystem model to understand the interplay between species composition of the forest, forest disturbance dynamics affected by climate change, and disturbance management. The tested measures included (a) active transformation of tree species composition toward site-matching species; (b) intensive removal of windfelled trees, which can support the buildup of bark beetle populations; and (c) reduction of mature and vulnerable trees on the landscape via modified harvesting regimes.
3. We found that management systems aiming to sustain the dominance of Norway spruce in the forest are failing under climate change, and none of the measures applied could mitigate the disturbance impacts. Conversely, management systems fostering forest diversity substantially reduced the level of disturbance. Significant disturbance reduction has been achieved even without salvaging and rotation length reduction, which is beneficial for ecosystem recovery, carbon, and biodiversity.
4. *Synthesis and applications:* We conclude that climate change amplifies the contrast in vulnerability of monospecific and species-diverse forests to wind and bark beetle disturbance. Whereas forests dominated by Norway spruce are not likely to be sustained in Central Europe under climate change, different management strategies can be applied in species-diverse forests to reach the desired control over the disturbance dynamic. Our findings justify some unrealistic expectations about the options to control disturbance dynamics under climate change and highlight the importance of management that fosters forest diversity.

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KEYWORDS
bark beetles, Central Europe, climate change, disturbance management, salvage logging, simulation model, tree species diversity

1 | INTRODUCTION

Forest disturbances are an integral part of forest dynamics, contributing to ecosystem functioning, creating heterogenous landscapes, and fostering biodiversity (Beudert et al., 2015; Turner et al., 2004). In production forests, however, disturbances place social management objectives at risk and compromise the provision of valued ecosystem services (Lindroth et al., 2009; Seidl & Blennow, 2012). Research suggests that all types of ecosystem services are negatively affected (Thom & Seidl, 2016), and these impacts will continue to increase in the future (Seidl, Schelhaas, Rammer, & Verkerk, 2014). Efforts to prevent or mitigate disturbance impacts have therefore become an integral part of forest management in Europe. The applied measures include, for example, improvement of tree vigor and morphology, modification of stand structure and composition, or reduction of fuel loads and breeding substrate for insects (Berryman, 1988; Gardiner & Quine, 2000; Jactel et al., 2009; Wermelinger, 2004). Research has also highlighted some controversies related to active disturbance management. These particularly include an effort to replace complex ecosystem regulation dynamics by oversimplified technological processes, which often erode ecosystem resilience (Cox, 2016) and produce collateral effects interfering with local management objectives (Leverkus, Lindenmayer, Thorn, & Gustafsson, 2018). For example, long-term outbreak prevention via salvage logging can increase forest vulnerability to future disturbances via creation of vulnerable complexes of mature stands with high growing stock (Dobor et al., 2020). Intensive disturbance management can also affect the quality of ecosystem services and modify natural ecological interactions in the forests (Leverkus, Lindenmayer, et al., 2018).

Forest disturbance management has received increased attention in response to the recently intensified disturbance regimes and the increased rate of social and ecological impacts (Müller, 2011; Senf et al., 2018). Moreover, model projections indicated that disturbance intensification will continue to increase in the future, which highlights the need to revise current management strategies (e.g., Dobor et al., 2019, 2020; Hlásny et al., 2019; Honkaniemi et al., 2020; Kausrud et al., 2012; Seidl et al., 2018). This requires a comprehensive understanding of the interactions between vegetation and disturbance dynamics affected by climate change, and management, which strives to interact with this overly complex and potentially unstable system. Quantifying the outcomes of disturbance management in ecosystems affected by climate change is therefore beyond our current understanding, which was mostly developed under past and more stable conditions.

Among different disturbance agents, bark beetles (Coleoptera: Curculionidae, Scolytinae) have shown remarkable climatic sensitivity (Cudmore et al., 2010; Seidl & Rammer, 2017). Recent intensification of bark beetle disturbance in Europe has been greater than that of any other disturbance type, including wind and wildfires (Seidl, Schelhaas, et al., 2014). While total canopy mortality has doubled in Europe over the last three decades (Senf et al., 2018), impact from bark beetles has increased by 600% (Seidl, Schelhaas, et al., 2014). These outbreaks highlight the prominent role of climate change as the driver of bark beetle disturbance (Bentz et al., 2019; Jönsson et al., 2009). In Europe's *Picea abies*—*Ips typographus* system, climate change increases the number of bark beetle generations, reduces winter mortality, and compromises fitness of host trees (Huang et al., 2019). Climate change also synchronizes the outbreaks over areas large several hundreds of kilometers via the large-scale impacts of regional climate extremes (Senf & Seidl, 2018). Outbreaks of *I. typographus* amplified by climate change thus represent one of the major threats to forestry economies and the environment in Europe (Grégoire et al., 2015; Komonen et al., 2011).

In Europe's production forests, management has traditionally strived to control bark beetle populations to prevent or mitigate their impacts (Berryman, 1988; Wermelinger, 2004). These measures either aim to directly control populations of bark beetles or to modify forest structure and composition to create environment that is less conducive to the outbreaks (Wermelinger, 2004). Direct control mainly endeavors to reduce the amount of breeding substrate for beetles by removing trees affected by wind, snow, and rime; remove infested trees from the forest prior to beetles' emergence; and reduce beetle populations using insecticides or various trapping devices (Faccoli & Stergulc, 2008; Stadelmann et al., 2013). Conversely, indirect control includes silviculture practices, which, for example, aim to reduce tree competition for resources using thinning, reduce the concentration of host trees via change in tree species composition, or modify harvesting regimes to reduce the share of mature and vulnerable trees (Björkman et al., 2015; Jactel et al., 2009; Zimová et al., 2020). Indirect control can also aim to modify the forest configuration on the landscape to reduce the connectedness of local bark beetle populations and complexes of host trees (Honkaniemi et al., 2020; Seidl et al., 2018).

Efficiency of outbreak management measures in reducing the level of tree mortality is generally not sufficiently understood to inform management decisions (Hlásny et al., 2019; Kausrud et al., 2012). Rare examples of quantitative assessments include the studies of Faccoli and Stergulc (2008) for pheromone traps, and Stadelmann et al. (2013) and Dobor et al. (2019, 2020) for salvage logging. This lack of quantitative understanding becomes critical if the outbreaks are amplified by climate change and management resources are becoming increasingly limited. Still, the consensus exists that species-diverse forest with complex structures show increased resistance to herbivores (Guyot et al., 2016) and have higher survival rates (Griess et al., 2012; Neuner et al., 2015). Adaptive change in tree species composition can dilute the host trees in the forest, increase semiochemical diversity, and strengthen resilience mechanisms (Seidl, 2014; Zhang

& Schlyter, 2003). Managing forests for diversity is thus recognized as a prominent strategy to mitigate bark beetle disturbance. Because the effect of silviculture management can be rather delayed, it can be applied concurrently with other measures such as salvage removal of windfelled trees, beetle trapping, or premature harvesting of vulnerable stands. Interactions of these effects may, however, generate hardly predictable nonadditive outcomes, which can be further modulated by climate change (Dobor et al., 2020).

Here, we investigate how management of functionally linked wind and bark beetle disturbances performs in differently managed forests, and how this performance can be affected by climate change. In particular, we investigated how adaptive change in tree species composition affects the vulnerability of forests dominated by *P. abies* to natural disturbances and how the transformation of species composition interacts with other disturbance management measures. We focused on Central Europe, which has become one of the hotspots of recent disturbance change, and where the revision of current disturbance management strategies is urgently required. Because this analysis requires considering landscape-scale climate-sensitive disturbance dynamics, disturbance interactions, and dynamic feedback from vegetation, we addressed these questions using the forest landscape and disturbance model iLand (Seidl et al., 2012).

2 | DATA AND METHODS

2.1 | Study region

The study area is in the Western Carpathians (the Low Tatras mountain range) in Slovakia (Lon 20.088–20.275, Lat 48.920–49.061), covering an area of 16,050 ha (Figure 1). The landscape has 70% forest cover and elevation range of 620 to 1550 m a. s. l. The forests are chiefly managed for softwood timber production, though recreation, game management, and nature conservation also occur.

Intense elevation and climate gradients, and the temperate continental climate (Kottek et al., 2006) resulted in the presence of multiple zonal forest communities in the natural species composition, with a dominance of broadleaved species (Rizman et al., 2005). Due to the intense production-oriented management applied over the last 200 years, however, the forests are currently dominated by Norway spruce (*Picea abies*), which is found (often in monocultures) across the majority of site types on the landscape (Figure 1). Other important tree species are European larch (*Larix decidua* Mill.), Scots pine (*Pinus sylvestris* L.), Silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.).

The current silvicultural system is an even-aged management regime with a rotation length of approximately 100 years. The primary approach to tree regeneration in stands with fir and/or beech admixtures is a uniform shelterwood cut, that is, progressive cutting that leads to the establishment of a new cohort of trees under the canopy of the retained mature trees. The shelterwood system contains 3 to 4 regeneration cuts applied over a period of approximately 30 years, followed by a final cut. In spruce monocultures, a small-scale clearcutting system is applied (cutblock size < 3 ha).

Recent years have been characterized by high natural disturbance activity, followed by high levels of salvage and sanitation felling. The natural disturbance regime consists of bark beetle (mainly *Ips typographus* L.) and wind disturbance, which has considerably intensified over the last 20 years.

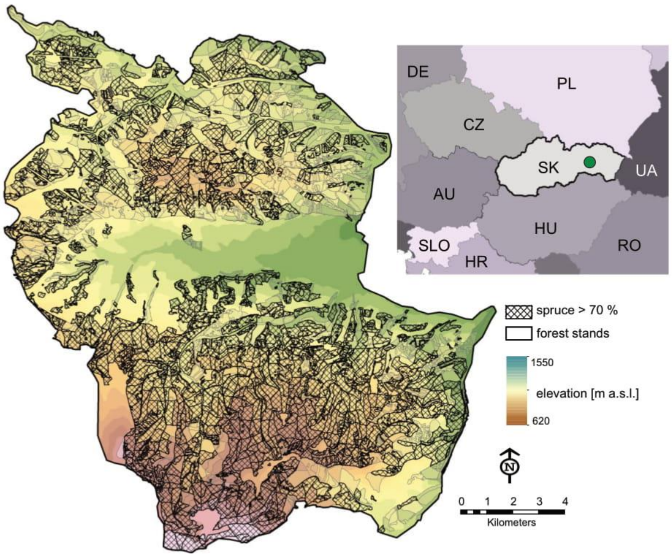

FIGURE 1 The study area: the Goat Backs Mt. landscape. Forest distribution and stands with the dominance of Norway spruce are indicated. Elevation is displayed in the background. The insert shows the location of the study landscape in Central Europe (green circle)

2.2 | Simulation model

We investigated the interactions between the climate, management, disturbances, and vegetation dynamics using the process-based model iLand (Seidl et al., 2012) (http://iland.boku.ac.at). iLand is an ecosystem model that simulates forest landscape dynamics, including growth and regeneration, disturbance dynamics, and management in a spatially explicit manner. The main entity in the model is a tree, for which the demographic processes are simulated. Processes at the stand and landscape scale constrain the dynamics of individual trees and thus allow for the scaling of tree-scale processes to large areas (Seidl et al., 2012). The model explicitly simulates tree competition for resources such as light, water, and nutrients. A light use efficiency approach (Landsberg & Waring, 1997) is used to simulate the production physiology. Carbon starvation is used as a process-oriented indicator of tree stress, which can result from competition for resources as well as suboptimal environmental conditions for tree growth (e.g., drought).

iLand's mechanistic representation of forest disturbances and vegetation dynamics, as well as the climatic sensitivity of these processes, makes it well suited for the research of disturbance dynamics under climate change (e.g., Dobor et al., 2018; Seidl & Rammer, 2017; Seidl, Rammer, & Blennow, 2014). Wind disturbances are initiated by the wind speed of severe wind events provided as an external input to the simulation. The wind impact is simulated iteratively, with the forest structure (including the appearance of new edges) being updated after each iteration in the event of breakage or windthrow (Seidl, Rammer, et al., 2014; Supplement A). The implementation of bark beetle disturbances considers bark beetle phenology and development, spatially explicit dispersal of beetles, colonization, and tree defense, as well as temperature-related overwintering success (Seidl & Rammer, 2017). Outbreaks are typically triggered by wind disturbance; salvage removal of windfelled trees can therefore be applied to reduce the outbreaks (Dobor et al., 2020). A detailed description of the implementation of wind and bark beetle disturbance in iLand is provided in Supplement A.

Flexible implementation of management operations, which include planting after harvests or natural disturbances, thinning, harvesting, and postdisturbance salvaging, allows for testing the effects of various disturbance management strategies (Dobor et al., 2019, 2020; Honkaniemi et al., 2020). iLand integrates an agent-based model of forest management (Rammer & Seidl, 2015), in which general stand treatment programs (i.e., a sequence of management interventions applied over the course of stand development) are dynamically adapted to the forest state emerging from the simulation. These features allow for testing the efficiency of measures taken in response to the simulated disturbance, considering the dynamically changing vegetation structure. The tested management interventions are implemented in the model as follows:

- Planting is applied after harvests and stand-replacing disturbances that affected a prescribed level of growing stock (75% in this study). Planting is based on prescriptions defining details of tree species, seedling dimensions, and spacing between the seedlings. Planting prescriptions can differ between stands, depending on site conditions or management objectives. The already established regeneration can be kept or removed.
- Thinning and harvesting are applied based on prescribed timing and intensity of removal. Different criteria on tree removal can be defined to implement practices such as clearcutting, shelterwood, or selection cut. Each stand has a stand treatment program assigned that defines the sequence of interventions.
- Salvaging is applied to harvest timber affected by disturbances. Different intensities of salvage removal can be prescribed, affecting forest carbon stocks, dynamics of secondary disturbances, and the deadwood patterns. The incidence of disturbances and subsequent salvage logging supersede regular management operations, resetting the default stand treatment program.

The model was extensively tested across a range of ecosystems in Europe and North America in previous studies (Honkaniemi et al., 2020; Silva Pedro et al., 2015; Thom et al., 2017). A detailed evaluation of simulated productivity, natural mortality, and regeneration patterns for the landscape studied here was conducted by Dobor et al. (2018). All testing exercises conducted for Central Europe proved good ability of the model to simulate ecosystem dynamics in this environment.

2.3 | Basic simulation setup

Prior to scenario simulations, an 800-year spin-up run was performed to estimate the initial litter, dead wood, and soil C pools. The spin-up run was also used to initialize stand structures in a manner consistent with the internal logic of the model. The procedure used assimilates information on the current composition and structure of forest stands (here based on forest management plan records; see Supplement B) to ensure that the resulting initial forest state for simulation is consistent with the model internal logic and represents the current structure and composition of the forest (see Thom et al., 2018 for details).

The scenario simulations were run for 100 years starting from the end-conditions of the preceding spin-up run. Each simulation was driven by five climatic scenarios (reference climate and four projected climates, see Supplement C). Each simulated forest development was exposed to five prescribed wind events, with parameters sampled from the distribution parameterized based on past meteorological observations for the area. The intensity of events was set to reach the average annual amount of disturbed trees recorded in the national forest disturbance statistics for the period 1990–2010, which range between 0.9 and 2.2 m^3 ha^{-1} $year^{-1}$ (Dobor et al., 2020; Konôpka et al., 2016). Each scenario run was replicated 10 times to account for the stochasticity in the simulations. The value of the so-called background infestation probability (a parameter related to bark beetle disturbance

TABLE 1 Tested combinations of disturbance management measures

Code	Management narrative	Planting scheme	Disturbance reduction actions		
			Change in species composition	Salvaging	Rotation length reduction
A	Reference management, focus on spruce timber production, no disturbance management action taken	Dominance of spruce seedlings (50%–70%, depending on site)	0	0	0
B1	A + reducing risk of disturbance via high-intensity salvaging		0	1	0
B2	A + reducing risk of disturbance via rotation length reduction		0	0	1
B3	A + reducing risk of disturbance via rotation length reduction and high-intensity salvaging		0	1	1
C1	Focus on adaptive change in species composition via planting on disturbed and harvested sites	Dominance of seedlings of nonspruce site-matching species (more than 80%, depending on site)	1	0	0
C2	C1 + reducing risk of disturbance via high-intensity salvaging		1	1	0
C3	C1 + reducing risk of disturbance via rotation length reduction		1	0	1
C4	C1 + reducing risk of disturbance via high-intensity salvaging and rotation length reduction		1	1	1

(Seidl & Rammer, 2017) was varied between the replicates in a range of 0.0005–0.0025 (Honkaniemi et al., 2020).

The implemented baseline management included tending, thinning, and harvesting, with timing and intensity of operations modeled after the management practice currently applied in the region (Halaj & Petráš, 1998). Depending on the site, 3–4 thinning operations were applied and rotation periods ranged from 90 to 140 years. In spruce monocultures, clearcut management was applied, whereas shelterwood management was simulated in mixed stands.

The simulations were run under the conditions defined by two regional climate models (RCM) driven by two Representative Concentration Pathway scenarios (RCP4.5 and RCP8.5). The RCMs were selected to represent the variability of climate change signal emerging from the large ensemble of climate projections developed in the frame of the CORDEX project (Giorgi et al., 2009) (Supplement C). A reference climate series was generated by randomly sampling years with replacement from the period 1996–2016.

2.4 | Disturbance management experiment

The previously described baseline management was modified to accommodate different combinations and settings of disturbance management actions. These include (a) targeted change in tree species composition via planting on cleared areas to reduce the overall forest vulnerability, (b) instant removal of windfelled trees, which can trigger or reinforce the outbreak of bark beetles, and (c) reduction of forest rotation length to reduce the proportion of mature trees, which are susceptible to both bark beetle and wind disturbance.

We organized these measures around two management narratives that are being intensively discussed in the Central European production forestry; (a) the industry demand-driven effort to maintain high proportions of Norway spruce in the forest, and (b) efforts to adapt the tree species composition to climate change and intensified disturbances via recovering natural species composition, which has been markedly altered over the last two centuries in many production forests in Central Europe (Klimo et al., 2000; Spiecker et al., 2004).

To address these two objectives, we implemented two seedling planting schemes on cleared areas. The first one promoted Norway spruce in species composition; depending on site, its share ranged from 50% to 70% (natural regeneration was, however, acting concurrently). The second one promoted site-suitable tree species following the natural species composition of the forest (after Rizman et al., 2005), which predominantly consisted of European beech, Silver fir, European larch, and pine. The share of Norway spruce did not exceed 20% in this planting variant.

We combined each of these planting variants with salvage removal of windfelled trees and the rotation length reduction. The salvaging was applied with 90% intensity, which was found by Dobor et al. (2019) to be the minimal intensity required to dampen the simulated outbreak of bark beetles. At the same time, such intensity represents a realistic approximation of the applied management practice. We simulated the reduction of the rotation length by 40% relative to the currently applied rotation (100 years for spruce stands, and 115 years for broadleaved species, on average). The rotation length was, however, not allowed to be <60 years. This level of reduction still conforms with the criteria for the production of softwood timber and can be expected to dampen the disturbance dynamics to a certain extent.

The disturbance reduction effect of different management actions was assessed by comparing the level of disturbed growing stock (m^3 ha^{-1} $year^{-1}$, average over the simulation period) reached under management variants B1 to C4 (Table 1) against the reference management A, which did not contain any disturbance management action. The total number of simulation runs in this experiment was as follows: 8 managements × 5 climates (four climate change scenarios and the reference climate) × 10 replicates, that is, 400 simulations.

3 | RESULTS

3.1 | Simulated disturbance patterns

The average level of wind disturbed growing stock simulated under the reference climate was 1.2–1.8 m^3 ha^{-1} $year^{-1}$ (range of eight management systems and 10 replicates), which falls into the observed range of 0.9–2.2 m^3 ha^{-1} $year^{-1}$. Under climate change, wind disturbance decreased by 11%–16% relative to the reference climate, which likely accounts for the competing interaction between wind and bark beetles (Figure 2a).

Each wind event triggered a multi-year bark beetle outbreak of varying size, depending on the actual amount of windfelled trees, weather, and stand conditions (Figure 2b; Supplement D). Under reference climate, disturbed growing stock was 1.6–3.0 m^3 ha^{-1} $year^{-1}$, that is, slightly exceeded the growing stock disturbed by the triggering windthrows. Climate change produced a strong amplifying effect on the outbreaks, and the level of growing stock disturbed exceeded the reference value by 239% under RCP4.5 and 310% under RCP8.5 (median increase, Figure 2).

3.2 | Disturbance management performance

Under the reference climate, the total level of growing stock disturbed was substantially reduced by different combinations of management measures (Figure 3a,b). In management systems promoting spruce in species composition, however, the mitigation effect highly varied within (i.e., the interreplicate variation) and between treatments. Still, the average reduction effect over the simulation period was 8% for salvaging, 3% for rotation length reduction, and 13% for the combination of latter two measures (separate effects on wind and bark beetle disturbance are provided in Supplement E).

Management systems promoting adaptive changes in tree species composition more efficiently reduced the disturbance than the previous systems, though lead times were long (from ca. 2060) (Figure 2b). The simultaneous application of different treatments amplified the disturbance reduction effect. Systems containing salvaging (C2 and C4) were most efficient, reducing the disturbance by 19%–25% relative to the reference treatment A (Figure 3c).

Climate change markedly altered patterns identified under the reference climate. Disturbance treatments were inefficient in

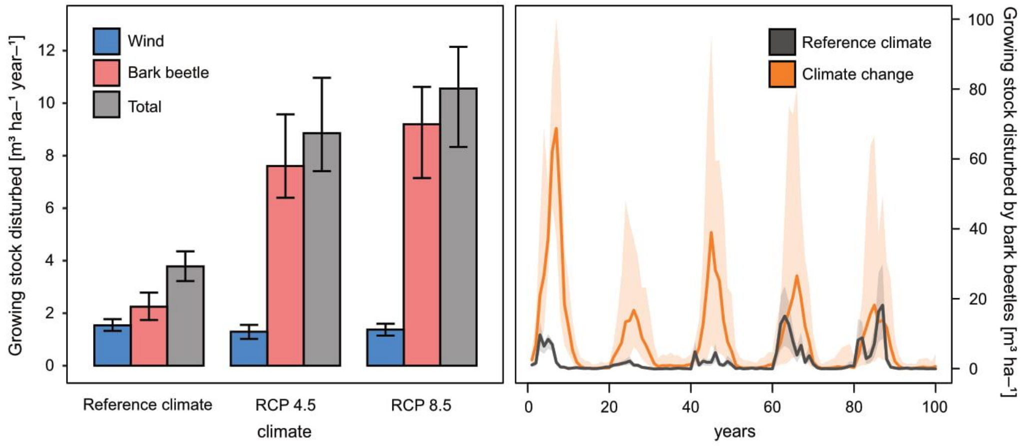

FIGURE 2 Growing stock disturbed by wind and bark beetles during the 100-year simulation period under reference climate and two groups of climate change scenarios driven by RCP4.5 and RCP8.5 (a). Medians and 10%–90% quantiles calculated from 10 replicate simulations, 8 management regimes, and 4 climate change scenarios are shown. (b) The temporal development of growing stock disturbed by bark beetles under the reference climate (averaged over managements and replicates) and climate change (averaged over managements, RCP scenarios, and replicates)

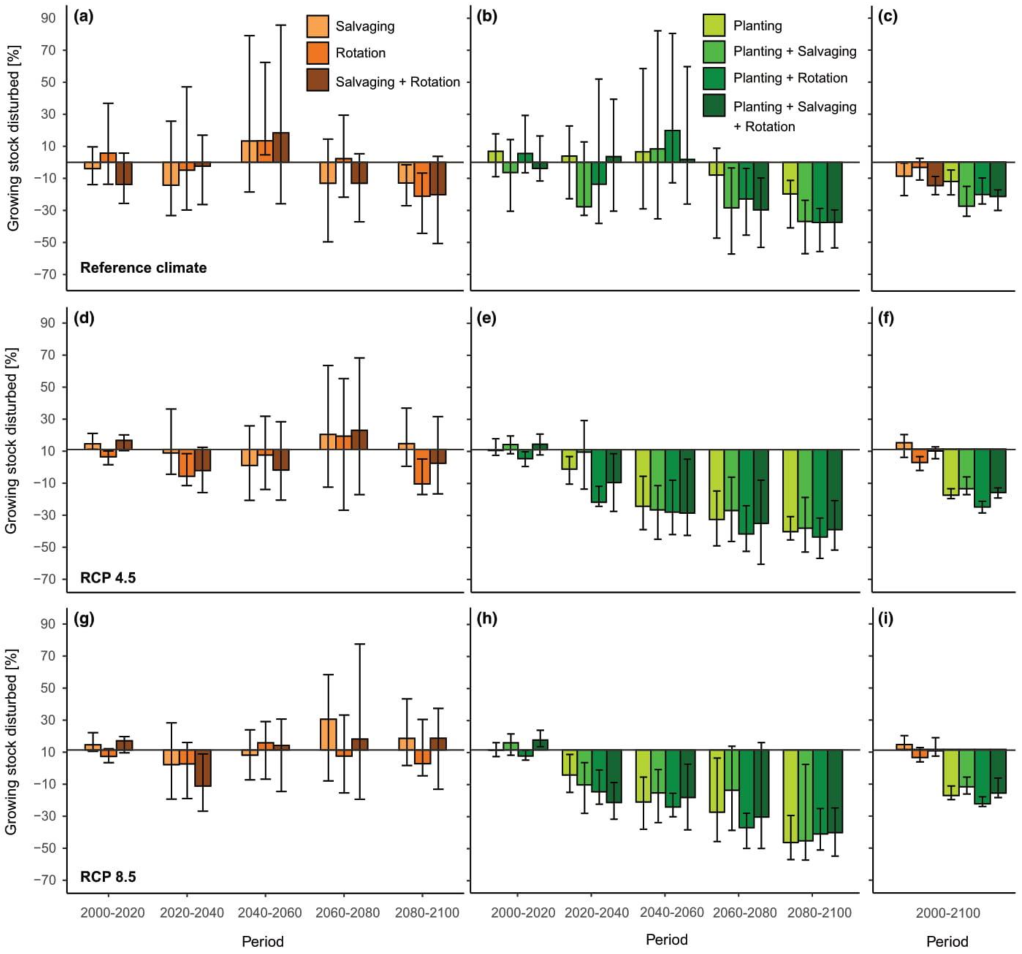

FIGURE 3 Relative differences between the level of growing stock disturbed by wind and bark beetles under management systems containing different combinations of disturbance management actions, and the baseline management, with no disturbance management actions. Management systems on the left (brownish) promote planting of spruce on disturbed and harvested stands, whereas systems on the right (greenish) promote adaptive changes in species composition by planting less vulnerable site-matching tree species

reducing disturbance impacts in management systems promoting spruce (Figure 2d,g). On the other hand, climate change amplified the efficiency of disturbance treatments in systems promoting adaptive changes in tree species composition. These measures started to be effective much earlier than under the reference climate; significant disturbance reduction started to be observed as soon as 2020. The combination of different measures did not significantly increase the disturbance reduction effect of changing tree species composition, particularly in the second half of the simulation period.

3.3 | Underlying changes in forest structure

The tested management interventions affected forest susceptibility to disturbance mainly via changes in forest age structure and species composition. The initially high proportion of Norway spruce persisted under the reference climate, when the level of disturbance was low (Figure 4). This persistence was supported by the dominance of spruce in planting. The modified planting scheme mainly caused the proportion of Silver fir and European beech to increase, while spruce remained dominant. Even a moderate climate change

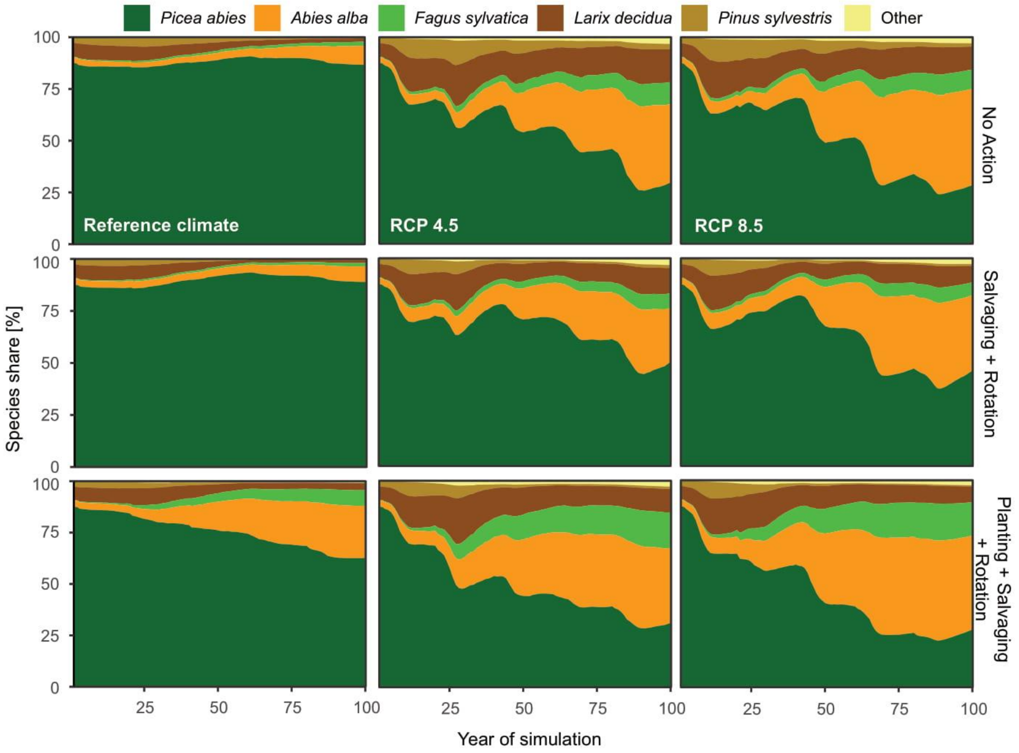

FIGURE 4 Development of tree species composition in the study landscape under different management and climate change scenarios. The upper row is the baseline management, which included no disturbance management actions and promoted spruce in planting on cleared areas. The middle row reflects an alternative to the baseline management, with salvage removal and rotation length reduction applied. The bottom row reflects the most proactive management, which promotes nonspruce species in planting, with intensive salvaging of windfelled trees and a reduced rotation length

(RCP4.5) caused spruce to decline sharply throughout the simulation period, and this decline was further amplified by the change in planting. The main replacement species were Silver fir, European beech, and European larch. Information about the remaining management variants is provided in Supplement F.

Forest age sharply decreased under management systems involving the reduction of rotation length compared to the reference management A (Figure 5). Whereas the decrease was gradual under reference climate, age fluctuation was more erratic under climate change and age reduction occurred faster. The reduction reached −20 to −30% of the initial forest age.

4 | DISCUSSION

Previous studies indicated that Norway spruce forests may not be sustained in many regions of Europe because of intensifying outbreaks of bark beetles, genetic maladaptation to future climates, and sensitivity to climatic stress (Frank et al., 2017; Marini et al., 2012; Seidl, Schelhaas, et al., 2014; Zang et al., 2014). The role of active management of forests disturbances, however, has not been included in these investigations although it is an integral aspect of European forest management (Berryman, 1988; Wermelinger, 2004). We showed that contrast in the vulnerability of monospecific forests and forests managed for diversity is considerably amplified by climate change. We also found that management measures that were successfully applied in the past are becoming inefficient under warmer climate amplifying the disturbance dynamics, which particularly applies to the forests dominated by Norway spruce.

4.1 | Implications for ecosystem management

We found that the studied ecosystem was relatively stable under past climate and the level of disturbance was low. Such dynamics agree with the national forest damage statistics (e.g., Gubka

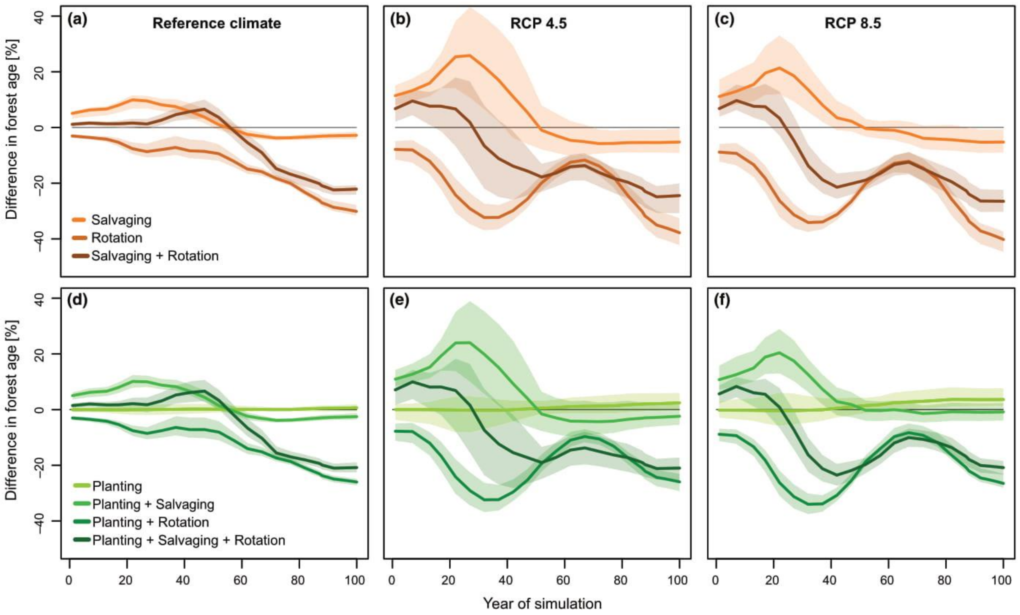

FIGURE 5 Differences between the mean forest age on the study landscape simulated under management systems involving different combinations of disturbance reduction measures and the reference management system, where no measures were applied. The upper row indicates management systems with a dominance of spruce in planting after harvests and disturbances. The bottom row indicates management systems promoting site-matching tree species

et al., 2013), which indicated that the level of disturbance was quite low before 1995. This suggests that intensively applied measures (planting, sanitary operations, etc.) managed to sustain the forest despite its structure and resilience being compromised by the previous long-term production-oriented management. In our study, these conditions correspond with simulation designs A and B1-B4 exposed to the reference climate.

Exposing the spruce dominated system to climate change increased the disturbance intensity by 140%–172% and caused the proportion of Norway spruce to decline sharply. Parallels can be drawn between this simulated development and the recently observed collapse of spruce forests in some regions of Europe—Central Europe being an epicenter—triggered by climate extremes and large-scale outbreaks of bark beetles (Hlásny et al., 2019; Senf & Seidl, 2018). Moreover, we found that this increase in disturbance intensity cannot be controlled by the here tested management measures, despite the measures being applied with a high intensity (90% removal of windfelled trees and 40% reduction of the rotation length). This is a striking difference from the disturbance management applied under past climate, where disturbance intensity was lower and it could have been further reduced by management. Conversely, we found that the forest managed for diversity showed lower disturbance rates even without applying any other measures (i.e., without the salvage removals and rotation length reduction). These findings provide a new perspective on the role of adaptive changes in species composition in disturbance management and can clarify some misconceptions about the transferability of past management tactics to the qualitatively new conditions produced by climate change.

Consistent with previous studies, we found that the change in tree species composition toward a higher proportion of less vulnerable and site-adapted species has paramount importance in managing forests under climate change (Jandl et al., 2019). Diverse ecosystems generally show lower disturbance rates compared with monospecific forests (Griess et al., 2012; Neuner et al., 2015) and are also superior in the provisioning of ecosystem services (Mori, 2017). Still, some previous studies suggested that the pest control effect may depend more on species composition of the forest than on diversity (Koricheva et al., 2006). Accordingly, the here presented disturbance mitigation effect needs to be considered as a function of both replacement of vulnerable Norway spruce by other tree species and the increase in stand- and landscape-scale diversity, which, for example, dilutes the host trees and prevents the large-scale spread of bark beetles (Honkaniemi et al., 2020; Silva Pedro et al., 2015).

We found that the same disturbance reduction effect can be reached by applying different management actions. This finding deserves recognition in forestry practice, because measures such as salvaging, modifying harvesting regimes or changing tree species composition affect ecosystem dynamics, and provision of ecosystem services in different ways (Leverkus, Benayas, et al., 2018; Roberge et al., 2016). Quantitative understanding of these measures thus allows formulating management strategies consistent with local management objectives. Notably, measures such as salvage removal of windfelled trees and rotation length reduction did not significantly amplify the disturbance reduction effect produced by mere change in species composition. This indicates that these measures could be potentially avoided, providing multiple benefits for forestry economies and natural ecosystem dynamics. For example, maintaining older conditions on the landscape (i.e., avoiding rotation length reduction) can be beneficial from the viewpoints of biodiversity, forest carbon, and landscape scenic values (Roberge et al., 2016; Thom et al., 2019). Maintaining deadwood in the forest (i.e., avoiding or reducing salvage removals) supports water and climate regulation functions, increases forest diversity, including pests' antagonists, and preserves deadwood carbon stocks (Lassauce et al., 2011). Therefore, complex considerations are needed to formulate a proper combination of disturbance management actions to reach the desired control over the disturbance dynamics and not to compromise important ecosystem services.

4.2 | Methodological aspects and limitations

Here, we used a highly complex simulation model to investigate the interactions between disturbance dynamics, management, vegetation feedbacks, and climate change. Although such an approach allowed identifying and attributing the effects of different management actions, the uncertainty related to the representation of individual processes and model assumptions needs to be carefully considered (Huber et al., 2020). Although the model's use is supported by numerous testing exercises that particularly addressed forest productivity, regeneration, and natural mortality (e.g., Dobor et al., 2018), reproducing complex disturbance regimes in models remains challenging (Seidl et al., 2011). High stochasticity of disturbance events complicates testing the simulation outputs against the observed impacts (but see for example. Seidl & Rammer, 2017). We here prescribed the intensity of wind impacts to match the long-term observations, whereas the simulated windthrow pattern and the interaction with bark beetle dynamics were simulated as emergent properties of the used simulation framework. More comprehensive testing of the simulated disturbance patterns against observation would provide useful support to the presented findings.

Given the high complexity of our experimental design, we only investigated one level or salvaging intensity and rotation length reduction, though management practice may require more complex information (see e.g., Dobor et al., 2019, 2020; Zimová et al., 2020). The tested intensities were, however, near to the logistic limits of the current forest management and can thus be interpreted as the reachable maximum under the operational management conditions.

The complexity of our design can be further increased by including other management variants, which stress, for example, adaptive changes in species composition, including altitudinal shift of zonal trees species (Moser et al., 2010) and introduction of species that do not participate in the actual species composition. In the Central European forestry, these species may include, for example, native oak species (*Quercus* sp.) which are expanding their ranges under climate change (e.g., Mette et al., 2013) as well as introduced species of which the Douglas fir (*Pseudotsuga menziensii*) has received considerable attention (Spiecker et al., 2019). Although such changes would not directly affect the disturbance dynamics in the current modeling framework (their vulnerability is similar to other species on the study landscape), they could indirectly affect the disturbance dynamics via different rates of establishment on disturbed sites.

5 | CONCLUSIONS

Management of wind and bark beetle disturbances constitutes an integral part of European forestry; yet, many approaches are based on plausible or intuitive narratives rather than on tested and data-driven concepts. We presented a new perspective on disturbance management in the Central European production forests and particularly on the interactions of adaptive changes in species composition with other management measures. Consistent with previous studies, we found a contrasting sensitivity of monospecific and species-diverse forests to disturbance impacts. However, we showed that climate change further amplifies this contrast and favors management fostering forest diversity, which can exert better control over disturbance dynamics even without pervasive measures compromising the biodiversity and resilience of the forest. These findings can justify some misconceptions about disturbance management under climate change and can support the formulation of improved management strategies.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

Laura Dobor: Formal analysis (equal); Methodology (equal); Software (equal); Visualization (equal); Writing-review & editing (equal). **Tomáš Hlásny:** Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Project administration (lead); Writing-original draft (lead); Writing-review & editing (lead). **Soňa Zimová:** Data curation (supporting); Formal analysis (equal);

Resources (equal); Software (supporting); Writing-review & editing (supporting).

DATA AVAILABILITY STATEMENT

Results are archived in the Zenodo open-access repository, http://doi.org/10.5281/zenodo.4020390. Additional information on the used ecosystem model, including the source code can be found at http://iland.boku.ac.at.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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5.5 Infection Levels of the Microsporidium *Larssoniella duplicati* in Populations of the Invasive Bark Beetle *Ips duplicatus*: From Native to New Outbreak Areas.

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Article

Infection Levels of the Microsporidium *Larssoniella duplicati* in Populations of the Invasive Bark Beetle *Ips duplicatus*: From Native to New Outbreak Areas

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Abstract: The microsporidium *Larssoniella duplicati* (Weiser, Holuša, Žižka, 2006) is a specific pathogen of the bark beetle *Ips duplicatus* (C.R. Sahlberg, 1836), which is a serious pest of Norway spruce (*Picea abies* (L.) H. Karst) in Europe. From 2011 to 2016, infection levels of *L. duplicati* and other pathogens in *I. duplicatus* populations were assessed along a gradient, ranging from areas in the north, where the beetle is native, to areas in the south, where the beetle has only recently invaded. The 21 study sites ranged in altitude from 229 to 1009 m a.s.l. We found that pathogen infection levels in *I. duplicatus* populations decreased from the native areas in the north to the new areas of beetle expansion in the south. We also found that pathogen level increased with altitude. The *L. duplicati* infection levels were not associated with the infection levels of other beetle natural enemies. The infection level decreased with the length of time of beetle establishment in an area. The infection level increased with the number of beetles trapped and dissected at a site.

Keywords: *Ips duplicatus*; pathogen; vector; infection level; invasion; latitude

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1. Introduction

Changes in climate and land use can increase the spread of organisms [1]. Many of these organisms are non-native to their new area of distribution; some spread to new areas but also increase their population densities in their former areas [2,3]. In some cases, such invasive species begin to damage habitats that are important for humans, like forests with fast-growing tree species [4]. One of the most commercially important tree species in Europe is the Norway spruce (*Picea abies* [5]). This tree is attacked by many species of bark beetles of which *Ips typographus* (Linnaeus, 1758) is the most important in terms of loss of mature trees before final cutting [6].

The double-spined spruce bark beetle *Ips duplicatus* is a native species in Scandinavia, eastern and northern parts of central Europe and northeast Asia, where it occurs on Norway spruce. The beetle is currently spreading to Norway spruce in many parts of Europe. Its high outbreak potential is

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supported by climatic change, the physiological weakness of trees, and the attack of such weakened trees by the fungus *Armillaria ostoyae* (Romagn. Herink, 1973) and other pathogens [7,8]. Current studies focusing on wind and bark beetle disturbances suggest increase damages in Europe under climate change [9–11]. The combination of increasing frequency of drought events, Norway spruce planting in non-native habitats and warmer temperatures are considered important predisposing factors triggering the double-spined spruce bark beetle outbreaks. As a result of these factors affected by climate change, the number of *Ips duplicatus* generations is increasing to two to three during one vegetation period in the central European area [12].

From the beginning of the 20th century, the beetle began spreading from its origin in the Palearctic region to the south because spruce monocultures were being increasingly established in the south in Europe [8], unlike most other bark beetle invasions that extend from south to north [13,14]. *I. duplicatus* was first noted in eastern Czech Republic and south Poland in 1960s [15–17]. That area experienced massive *I. duplicatus* outbreaks in the 1990s. During the last 200 years, Norway spruce has been planted in many areas of Europe, mainly out of the natural range of this tree. As the planted trees are growing out of their natural range, they may be stressed [18], and this has increased the spread of *I. duplicatus* to southern Europe [19]; *I. duplicatus* has even been recorded in south Slovakia [15,20] and throughout Romania [21].

The microsporidium *Larssoniella duplicati* appears to be a specific pathogen of *I. duplicatus*; its presence in other spruce bark beetles, such as *I. typographus*, *Pityogenes chalcographus* (Linnaeus, 1761), and *Ips amitinus* (Einchoff, 1871), has not been reported [22–24]. This specificity of *L. duplicati* is not as usual among pathogens of bark beetles; i.e., the same pathogen usually occurs in multiple bark beetle species, but other examples are known [25–29].

L. duplicati was first described in the Czech Republic and Poland [24], where its infection levels in *I. duplicatus* populations are stable and where the disease is probably chronic [22]. This microsporidium infects the midgut muscularis, the ovaries, and the Malpighian tubules of adult beetles. The infection is always in the infected tissue, because infected muscle fibres hold the spores in position [24]. Its infection levels in the native area of beetle (Scandinavia) and the new outbreak area (Romania) have not been studied [23].

The current study had two objectives. The first was to compare the infection levels of *L. duplicati* in the native and new outbreak areas of *I. duplicatus* in Europe. The second objective was to identify variables associated with differences in *L. duplicati* infection levels in *I. duplicatus* populations.

2. Materials and Methods

Pathogens of *I. duplicatus* were studied at 21 sites: four in the Czech Republic, five in Romania, eight in Poland, and four in Sweden. The altitudes of study sites ranged from 229 to 1009 m a.s.l. (Figure 1). During the years of 2011–2016, beetles were collected using Theysohn pheromone traps (Theyson Kunststoff. GmbH, Germany) or Intercept traps (only in Romania) baited with pheromone lures ID Ecolure (FYTOFARM Group s.r.o., Slovakia), Pheagr IDU (Sci-Tech, s.r.o, Czech Republic), Duplodor (Chemipan, Poland), or an experimental lure (Romania) [30] (Table 1). In all used pheromone lures, the main compound is always E-myrcenol—the main aggregation pheromone component for *I. duplicatus* [31]. The pheromone lures were changed after 10 weeks. Each site was sampled in only 1 or 2 years.

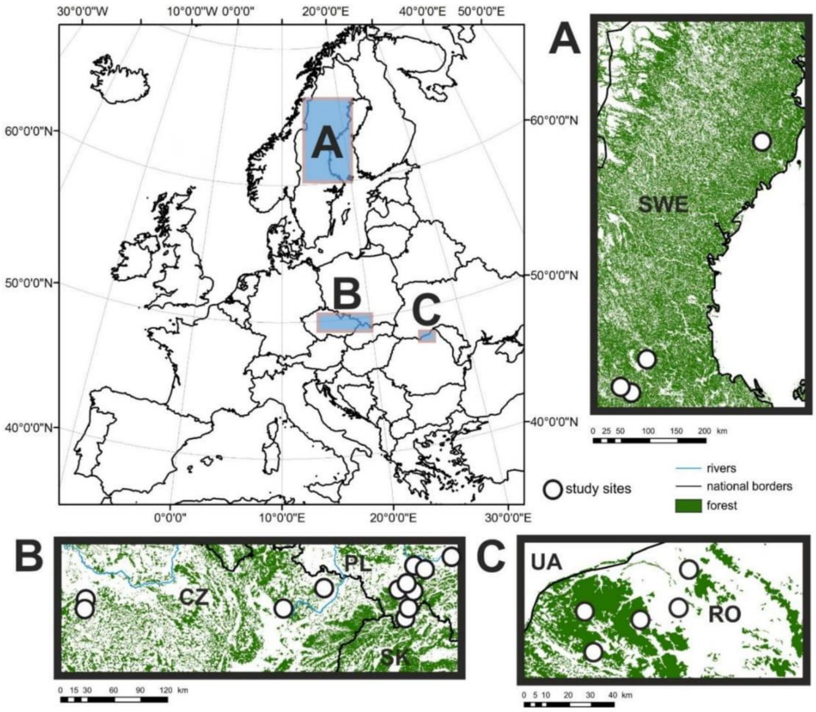

Figure 1. Study sites (circles) in Europe where *Ips duplicatus* was collected during 2011–2015 in forest areas (green).

Beetles were collected from the beginning of May to the end of August. In the study sites, flight barrier traps were placed 1.5 m above the ground and approximately 15–20 m from a standing spruce tree that was more than 30 years old. All forest stands at study sites were composed of a mosaic of trees of all ages, so there was enough suitable material for *Ips duplicatus* infestation.

Trapped beetles were placed in Eppendorf micro-test tubes with a piece of damp gauze to maintain humidity. The tubes were stored frozen until the beetles were dissected.

Each beetle was identified to species [32] and then dissected by removing the gut, Malpighian tubules, ovaries, and the body fat. The dissected tissues were examined with a light microscope (Nikon Eclipse 50 Ni, Nikon Instruments Inc., Melville, NY, USA) at 40 to 400× magnification to determine the presence of *L. duplicati* (oval spores of two sizes, 3–3.5 × 1.5–2 and 2–2.5 × 1.5 in intestinal muscles) and other pathogens and nematodes.

Data concerning the distribution of coniferous forests relative to the study sites were obtained from [32] and were corrected using Corine Land Cover. The program ArcMap 10.0 (ESRI, Redlands, CA, USA) was used to create Figure 1, which shows the distribution of the study sites.

Basic statistical analyses were performed in Statistica 13.1 (Dell software, Austin, TX, USA). We used the Shapiro Wilk test to determine the normality of the data (infection level). The Wilcoxon matched pair test was used to compare infection levels between sexes (percentages of infected males vs. females). Non-parametrical analyses were used as a control for the potential influence of local differences in infection levels at the country level.

Detailed analyses were done in SAM v4.0 [33]; we computed Moran's I to assess the spatial autocorrelation of our dependent variable (infection level of *L. duplicati*) in seven distance classes.

We assessed the relationships between infection level of *L. duplicati* (the percentage of infected individuals at a site, and the dependent variable) and the following independent variables: altitude, latitude (north-south gradient), longitude (east-west gradient), infection level of *Chytridiopsis typographi* parasitism by intestinal nematodes, parasitism by hemolymph nematodes, number of *I. duplicatus* beetles captured and dissected, and year (time of beetle collection). For linear regression of infection level on independent variables, infection level data were arcsine square root transformed to obtain normality. Analyses of the interaction among studied independent variables indicated multicollinearity for longitude (VIF = the variance inflation factor >2), which was the variable that described the east-west gradient in outbreak area of *I. duplicatus*. Thus, longitude was not further analysed. As some independent variables were not significant, we selected variables for inclusion in the final model based on AICc (Akaike information criterion with correction for small sample sizes) as implemented in SAM. In further analyses of *L. duplicati*, we used seven independent variables: latitude (north-south gradient); the infection level of the microsporidium *Chytridiopsis typographi*; the parasitism by intestinal nematodes; the parasitism by nematodes in hemolymph (hereafter termed hemolymph nematodes); the altitude of the study site; the number of *I. duplicatus* beetles trapped and dissected at a site; and the year of beetle collection.

Table 1. Background information on the study sites where *I. duplicatus* specimens were collected and assessed for pathogen infection. Country of origin (Country): Sweden (SWE), Poland (PL), Czech Republic (CZ), Romania (RO). In traps were used different pheromone lures: ID Ecolure, Duplodor, Pheagr IDU and in Romania the experimental lure (exp. lure) [30].

Study Sites	Country	GPS Coordinates		Year of Collection	Pheromone Lure	Altitude (m a.s.l.)
		N	E			
Nås	SWE	60.4677	14.5003	2014	ID Ecolure	232
Siljansfors	SWE	60.9730	15.0578	2014	ID Ecolure	324
Vansbro	SWE	60.5229	14.2389	2014	ID Ecolure	229
Vindeln	SWE	64.2000	19.7833	2014	ID Ecolure	291
Petkówka	PL	49.7333	19.2333	2015; 2016	Duplodor	668
Rajcza	PL	49.7666	19.2333	2015; 2016	Duplodor	646
Romanka Górna I	PL	49.5805	19.2246	2016	Duplodor	829
Romanka Górna II	PL	49.9338	19.3989	2015	ID Ecolure	1009
Sopotnia Dolna	PL	49.9350	19.4664	2015	ID Ecolure	953
Tokarnia	PL	49.9833	19.9833	2015	ID Ecolure	688
Ujsoły	PL	49.7508	19.2009	2015; 2016	Duplodor	859
Złatna	PL	49.4833	19.1666	2015	ID Ecolure	638
Hlubočky	CZ	49.6920	17.4146	2013	ID Ecolure	382
Jílové u Prahy I	CZ	49.8866	14.5055	2016	Pheagr IDU	354
Jílové u Prahy II	CZ	49.9166	14.5071	2016	Pheagr IDU	457
Pustá Polom	CZ	49.8510	18.0242	2014	ID Ecolure	454
Calafindești	RO	47.8513	26.1459	2011	exp. lure	497
Ionu	RO	47.6134	25.4817	2013	exp. lure	1080
Solca	RO	47.7000	25.7963	2013	exp. lure	625
Sucevița	RO	47.7767	25.4817	2013	exp. lure	605
Todirești	RO	47.7127	26.0328	2013	exp. lure	415

3. Results

A total of 1539 adults of *I. duplicatus* from the 21 study sites located throughout the Czech Republic, Romania, Poland, and Sweden were dissected and analyzed.

The *L. duplicati* infection level in *I. duplicatus* populations (i.e., the percentage of specimens at a site with *L. duplicati*) across all countries averaged ± standard error (SE) 16.7% ± 8.4% and ranged from 0% to 39.1%. *L. duplicati* was detected in 20 of the 21 sites (Table 2). *L. duplicati* infection levels did not significantly differ between *I. duplicatus* sexes ($Z = 1.33$, $p > 0.05$). Infection occurred only in the intestinal muscles of *I. duplicatus*.

Table 2. Infection levels of four pathogens in *I. duplicatus*. Infection level refers to the percentage of beetles with the indicated pathogen. The location of the study site (Country): Sweden (SWE), Poland (PL), Czech Republic (CZ), Romania (RO). For each study site there is a number of inspected beetles (N) and infection levels of: *Larssoniella duplicati* (*L.d.*), *Chytridiopsis typographi* (*C.t.*), parasitism by intestinal nematodes (I.n.) and hemolymph nematodes (H.n.).

Study Sites	Country	N	*L.d.* (%)	*C.t.* (%)	I.n. (%)	H.n. (%)
Nås	SWE	46	39.1	-	15.2	-
Siljansfors	SWE	70	21.4	1.43	10.0	4.3
Vansbro	SWE	156	16.7	-	3.2	1.3
Vindeln	SWE	72	23.6	-	11.1	5.6
Petkówka	PL	107	19.6	-	3.8	4.6
Rajcza	PL	103	13.6	-	14.1	5.5
Romanka Górna I	PL	27	7.4	-	14.8	-
Romanka Górna II	PL	192	20.8	-	4.7	7.3
Sopotnia Dolna	PL	35	25.7	-	5.7	2.9
Tokarnia	PL	139	19.4	-	6.5	3.6
Ujsoły	PL	22	9.1	-	13.6	9.1
Złatna	PL	20	10.0	-	10.0	-
Hlubočky	CZ	22	13.6	-	18.2	4.6
Jílové u Prahy I	CZ	18	-	-	5.6	-
Jílové u Prahy II	CZ	43	7.0	2.3	4.7	4.7
Pustá Polom	CZ	237	27.4	0.8	10.1	1.7
Calafindești	RO	20	20.0	-	10.0	-
Ionu	RO	33	18.2	-	12.1	3.0
Solca	RO	80	11.3	-	3.8	3.8
Sucevița	RO	45	8.9	-	13.3	6.7
Todirești	RO	52	1.9	-	5.8	9.6

Average levels of *L. duplicati* infection did not significantly differ among countries (H = 4.96; $p > 0.05$). The *L. duplicati* infection level increased from south to north, averaging 12.1% ± 6.5% in Romania, 15.7% ± 6.1% in Poland, 16.1% ± 8.5% in the Czech Republic, and 25.2% ± 8.4% in Sweden (Table 2).

The microsporidium *Chytridiopsis typographi* ((Weiser, 1954) Weiser, 1970) was found at only three study sites, and these were in the Czech Republic and Sweden. Its infection levels were very low (Table 2).

In contrast, nematodes were found in *I. duplicatus* at 21 study sites. The parasitism rate ranged from 3% to 16% for intestinal nematodes and from 0% to 10% for hemolymph nematodes (Table 2). For both kinds of nematodes, average parasitism rate did not significantly differ among countries (intestinal nematodes: H = 0.08; $p > 0.05$; nematodes in the hemolymph: H = 0.81; $p > 0.05$).

The spatial autocorrelation for *L. duplicati* infection levels was not significant (Table 3). This indicated that infection levels tended to be randomly distributed in space, without a tendency toward clustering or regular spacing. The expected Morans I value was −0.06.

Table 3. Statistics for spatial autocorrelation analysis of *L. duplicati* infection levels in *I. duplicatus* populations at the 21 sites in Europe.

Distance Class	Distance Centre	Moran's I	*p*
1	45.2	0.1	0.6
2	306.6	0.1	0.7
3	650.3	−0.2	0.2
4	877.8	−0.1	0.6
5	1137.8	0.1	0.7
6	1510.1	−0.1	0.9
7	1975.8	−0.4	0.1

In regression analyses, the *L. duplicati* infection level was significantly related to altitude, latitude, year, numbers of dissected beetles, and the infection level of all other pathogens (F = 6.63; $p < 0.01$; Table 4). A regression model with all of the variables listed in Table 4 (significant and non-significant) explained a total of 71.2% of the adjusted variance in the *L. duplicati* infection level. The *L. duplicati* infection level was not significantly related with the infection levels of *C. typographi*, parasitism by intestinal nematodes, or hemolymph nematodes. The *L. duplicati* infection level significantly increased with latitude, altitude, and the number of beetles captured and dissected at a site, but significantly decreased with the year of the study (Table 4).

Table 4. Results for a regression model describing the relationship between the *L. duplicati* infection levels in *I. duplicatus* populations and the following variables: latitude (north-south gradient); infection level of *C. typographi*; parasitism by intestinal nematodes; parasitism by hemolymph nematodes (i.e., nematodes detected in the hemolymph); altitude; number of *I. duplicatus* beetles captured and dissected; and year (date of beetle collection). Variance Inflation Factor (VIF), corrected Akaike's Information Criterion (AICc) = −11.93. Significant variables are in bold.

Variable	VIF	*t* Value [a]	*p* Value
Constant		**3.1**	**0.01**
Latitude	**1.1**	**3.5**	**0.01**
C. typographi	1.3	1.4	0.18
Intestinal nematodes	1.4	0.8	0.43
Nematodes in hemolymph	1.1	−0.8	0.46
altitude	**1.4**	**3.8**	**0.01**
number	**1.1**	**2.9**	**0.02**
year	**1.6**	**−3.4**	**0.01**

[a] Positive and negative *t* values indicate positive and negative associations, respectively.

In the next step of the statistical analysis, we deleted non-significant variables from the model; the resulting model explained 70.1% of the adjusted variance in (r^2adj = 0.701; Table 5). We found that only significant variables from the previous regression left in the model and their *p* values were more significant, except of number of dissected beetles.

Table 5. Results of the model that best described (delta AICc <2 based) the relationship between the *L. duplicati* infection level in *I. duplicatus* populations (arcsine square root transformed). The best model included four predictor variables: latitude (north-south gradient); altitude; number of *I. duplicatus* beetles captured and dissected; year (date of beetle collection). Variance inflation factor (VIF). Corrected Akaike's Information Criterion (AICc) = −25.95 (significant variables are in bold).

Variable	VIF	*t* Value	*p* Value
Constant		**3.9**	**0.002**
Latitude	**1.0**	**4.0**	**0.002**
Altitude	**1.2**	**3.7**	**0.002**
Number	**1.0**	**2.8**	**0.020**
Year	**1.1**	**−3.9**	**0.002**

4. Discussion

The current research studied the species-specific pathogen *L. duplicati* associated with the double-spined spruce bark-beetle in areas where *I. duplicatus* is native, as well as in areas where *I. duplicatus* is newly established in Europe. We found two interesting patterns: *L. duplicati* infection levels in *I. duplicatus* populations significantly decreased across the latitudinal gradient from the north to the south and significantly increased with increasing altitude.

In the areas where *I. duplicatus* is native, the *L. duplicati* infection level was as high as 30%; in the areas experiencing new outbreaks of the beetle, infection levels varied around 10% [34]. In the current study, the highest infection level was 39.1%, and the infection level was higher than 10% at most of the study sites, what is consistent with previous reports [22–24]. The spatial distribution of infection levels was not influenced by the spatial arrangement of the study sites (i.e., sites with high or low infection levels did not tend to cluster in space). This was true even though some of the sites, especially those in Poland and the Czech Republic, were located near areas with spruce forests that have been highly stressed by drought and fungal diseases. Such stressed forests typically support higher population densities of *I. duplicatus* than non-stressed forests [20,35]. Generally, latitude-altitude gradient can be explained by increasing number of individuals in population at northern study sites and in long-term outbreak areas. Study sites with more abundant populations of bark beetles are collected more often and with higher infection levels of pathogens [36].

We also suspect that *L. duplicati* may influence the invasive potential and spread of *I. duplicatus*. This is because *L. duplicati* is likely to reduce the fitness of the infected beetles and infection level is growing more slowly in the newly established outbreak areas. In addition to being infected by *L. duplicati*, *I. typographus* and related bark beetles are also attacked by ectoparasitoids and by the pathogen *Mattesia schwenkei* Purrini, 1977. Infection level of this antagonists of *I. typographus* had lower infection levels in areas with new outbreaks of the beetle than in areas with long-lasting outbreaks (more than 10 years) of the beetle [37]. When bark beetle numbers are low or when contacts between individuals in breeding systems are limited, e.g., as is the case in managed forests, there is a reduced probability of pathogen transmission and therefore a low infection level of some common pathogens [23].

The infection level of *L. duplicati* increased with the number of individuals dissected at a site. Nevertheless, the infection levels do not change with changes in host population density [22–24,34], which suggests that transmission is vertical rather than horizontal [23], as it is for some other microsporidium pathogens [29,38]. Therefore, it is unclear why the infection level should increase with number of analyzed beetles of *I. duplicatus.* In the case of horizontally transmitted pathogens, the infection levels sometimes double or triple during the beetle reproductive period of even one generation [39]. In the current study, the main factor associated with low *L. duplicati* infection levels in *I. duplicatus* was the length of time that the area had been infested with the beetle. This effect of time since beetle establishment is somewhat unclear in the current study, however, the latter factor was confounded with collection date.

I. duplicatus produces only one generation per year in the boreal forests and in northern Poland [8,40] but up to three generations per year in Central Europe [12,15,41]. Although new outbreaks of *I. duplicatus* occur only sporadically at higher altitudes [16,20,42–44], the *L. duplicati* infection level was related to altitude in the current study. This could be explained by the relationship between latitude and altitude, i.e., the more southern sites had both low infection levels and low altitudes.

We also found that the *L. duplicati* infection level did not differ between *I. duplicatus* sexes or among the studied countries, which is consistent with previous reports for *L. duplicati* as well as for other pathogens of bark beetles [39,45].

The only insignificant relationships between *L. duplicati* infection levels and the other variables were with the infection levels of *C. typographi*, parasitism by intestinal nematodes, and hemolymph nematodes. Nematodes and *C. typographi* are the most frequently reported antagonists of *I. duplicatus* [23,26,27,46]. The infection level of *C. typographi* is often very low [23]. In our study, we found *C. typographi* at only three sites, and infection was always less than 2.4%, suggesting that *C. typographi* was probably not affecting *I. duplicatus* population density. Parasitic nematodes are commonly associated with *I. duplicatus*, occurring in more than 70% of the beetle's gallery systems [46–49]. As in the case of *C. typographi*, nematodes did not appear to affect *L. duplicati* infection levels.

5. Conclusions

L. duplicati is probably a chronic pathogen of *I. duplicatus* and might have little or even no negative effect on the beetle—especially out of the native distribution area of its host. This microsporidium may negatively influence the flight capability of pioneer beetles and their ability to successfully invade new host trees, but in time (few years) the infection level of this microsporidium increases in a new population and the differences are minimized. The infection levels of *L. duplicati* in *I. duplicatus* populations decreased with latitude; it was highest in the north (Sweden), where the beetle is native, and was lowest in the south (Romania), where the beetle has only recently invaded. This is most probably connected with colonization aspect of a new sites. Infection levels increased with altitude, but the effect of altitude was confounded with the effect of latitude.

The most important conclusions of our research on an alien pest and its pathogen is that they follow a latitude-altitude gradient. This most probably reflects fact that spread of pathogen is prolonged (e.g., similar to known escape from enemies' hypothesis in bark beetles) [50]. Nevertheless, altitude in coincidence with latitude, indicate some climatic limits of the pathogen—as north sites and high elevations are often more cold and wet than the opposite. This is also important regarding pest management. Even if *L. duplicati* does not have a strong impact on alien bark beetle, its virulence could have some impact on invasive success of the bark beetle.

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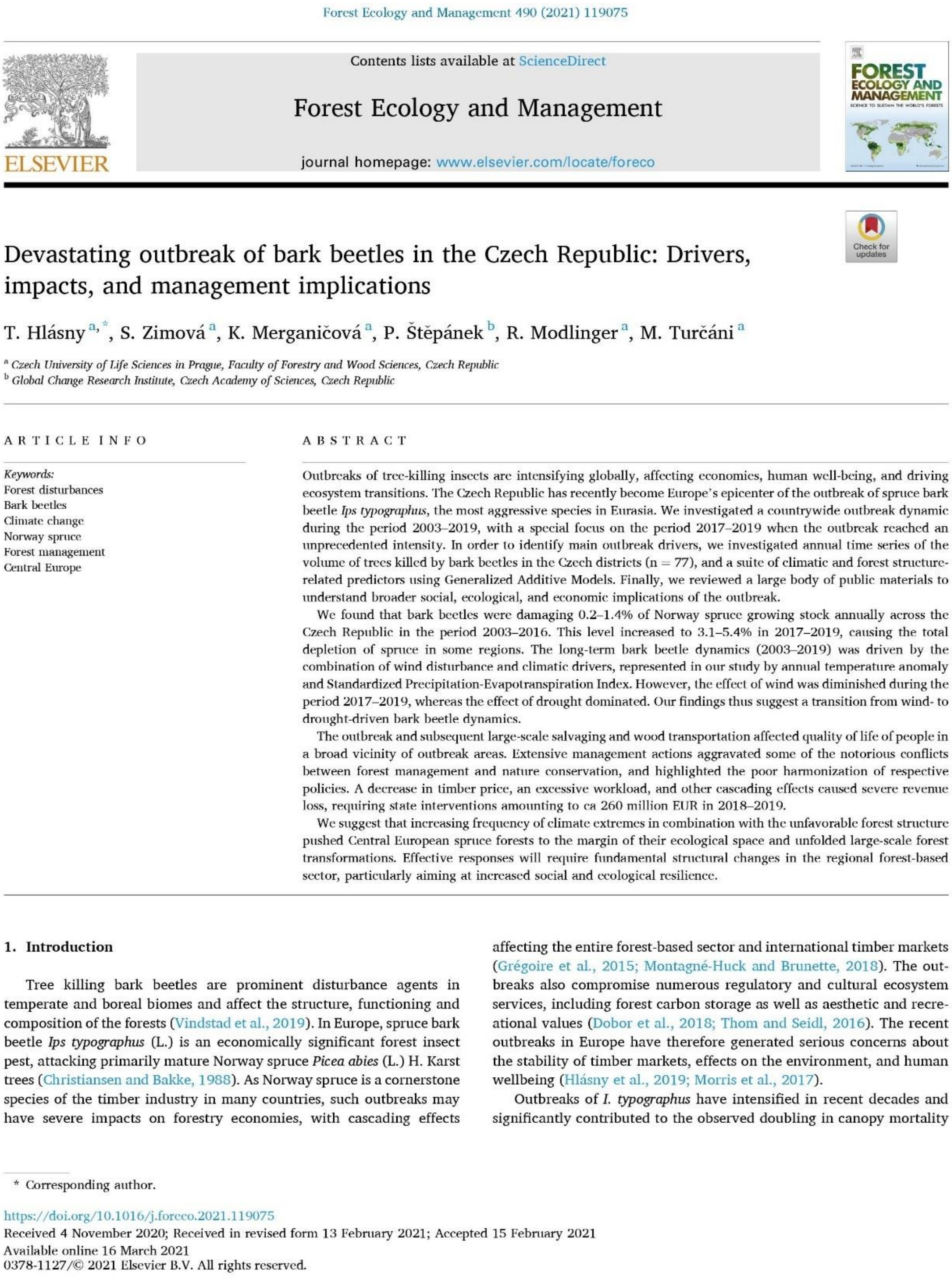
5.6 Devastating outbreak of bark neetles in the Czech Republic: Drivers, impacts, and management implications.



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Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications

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ABSTRACT

Outbreaks of tree-killing insects are intensifying globally, affecting economics, human well-being, and driving ecosystem transitions. The Czech Republic has recently become Europe's epicenter of the outbreak of spruce bark beetle *Ips typographus*, the most aggressive species in Eurasia. We investigated a countrywide outbreak dynamic during the period 2003–2019, with a special focus on the period 2017–2019 when the outbreak reached an unprecedented intensity. In order to identify main outbreak drivers, we investigated annual time series of the volume of trees killed by bark beetles in the Czech districts (n = 77), and a suite of climatic and forest structure-related predictors using Generalized Additive Models. Finally, we reviewed a large body of public materials to understand broader social, ecological, and economic implications of the outbreak.

We found that bark beetles were damaging 0.2–1.4% of Norway spruce growing stock annually across the Czech Republic in the period 2003–2016. This level increased to 3.1–5.4% in 2017–2019, causing the total depletion of spruce in some regions. The long-term bark beetle dynamics (2003–2019) was driven by the combination of wind disturbance and climatic drivers, represented in our study by annual temperature anomaly and Standardized Precipitation-Evapotranspiration Index. However, the effect of wind was diminished during the period 2017–2019, whereas the effect of drought dominated. Our findings thus suggest a transition from wind- to drought-driven bark beetle dynamics.

The outbreak and subsequent large-scale salvaging and wood transportation affected quality of life of people in a broad vicinity of outbreak areas. Extensive management actions aggravated some of the notorious conflicts between forest management and nature conservation, and highlighted the poor harmonization of respective policies. A decrease in timber price, an excessive workload, and other cascading effects caused severe revenue loss, requiring state interventions amounting to ca 260 million EUR in 2018–2019.

We suggest that increasing frequency of climate extremes in combination with the unfavorable forest structure pushed Central European spruce forests to the margin of their ecological space and unfolded large-scale forest transformations. Effective responses will require fundamental structural changes in the regional forest-based sector, particularly aiming at increased social and ecological resilience.

1. Introduction

Tree killing bark beetles are prominent disturbance agents in temperate and boreal biomes and affect the structure, functioning and composition of the forests (Vindstad et al., 2019). In Europe, spruce bark beetle *Ips typographus* (L.) is an economically significant forest insect pest, attacking primarily mature Norway spruce *Picea abies* (L.) H. Karst trees (Christiansen and Bakke, 1988). As Norway spruce is a cornerstone species of the timber industry in many countries, such outbreaks may have severe impacts on forestry economies, with cascading effects affecting the entire forest-based sector and international timber markets (Grégoire et al., 2015; Montagné-Huck and Brunette, 2018). The outbreaks also compromise numerous regulatory and cultural ecosystem services, including forest carbon storage as well as aesthetic and recreational values (Dobor et al., 2018; Thom and Seidl, 2016). The recent outbreaks in Europe have therefore generated serious concerns about the stability of timber markets, effects on the environment, and human wellbeing (Hlásny et al., 2019; Morris et al., 2017).

Outbreaks of *I. typographus* have intensified in recent decades and significantly contributed to the observed doubling in canopy mortality

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in Central Europe (Seidl et al., 2014; Senf et al., 2018). Climate is an important driver of such dynamics due to the ectothermic physiology of bark beetles (Jakoby et al., 2019). Climate controls the timing of bark beetle phenology, number of annual generations, and winter mortality (Baier et al., 2007; Marini et al., 2017). Climate also affects the conditions of host trees and their susceptibility to bark beetle attacks (Huang et al., 2020; Netherer et al., 2015). Interactions between the climatically sensitive development of bark beetles, the fitness of host trees, and the availability of breeding substrate determine whether bark beetle populations can cross the epidemic threshold and unfold the outbreak (Raffa et al., 2008). Recent changes in climate, which included an increased air temperature, changed precipitation patterns, and an increased frequency of heat and drought spells have thus critically amplified bark beetle outbreaks in Europe (Marini et al., 2017). Climate extremes not only intensify the outbreaks but also cause their large-scale synchrony (Seidl et al., 2016a). Model projections indicate that outbreak intensity will continue to increase in the coming decades, causing a large-scale transformation of forest landscapes with implications for the entire forest-based sector (Albrich et al., 2020; Dobor et al., 2020a; Honkaniemi et al., 2020). In Europe climate change is expected to increase the level of bark beetle disturbance sevenfold up to 2030 compared to the period 1971–1980 (Seidl et al., 2014). Other studies have suggested an increase in bark beetle disturbance during the 21st century by 60–220%, depending on the level of climate forcing and forest conditions (e.g. Dobor et al., 2020a, 2020b; Sommerfeld et al., 2020).

The other factor driving the recent outbreak intensification is the historical transformation of the forest structure (Munteanu et al., 2015; Seidl et al., 2011; Sommerfeld et al., 2018). In Central Europe, Norway spruce has been extensively planted outside the range of its native distribution at the expense of other, mostly broadleaved species to meet the requirements of expanding industries (Klimo et al., 2000; Spiecker et al., 2004). The prevalence of clear-cutting and long-term prevention of forest disturbances further homogenized the forest structure and increased the level of forest growing stock (Dobor et al., 2020a). Such management created large forest areas susceptible to an array of disturbances with eroded resilience mechanisms (Hanewinkel et al., 2008). The coincidence of such an unfavourable forest structure with erratic changes in climate may cause the limits of ecological resilience (tipping points; Dakos et al., 2019) to exceed and large-scale forest transformations to unfold (Albrich et al., 2020; Scheffer et al., 2009; Turner et al., 2020). Sommerfeld et al. (2018) suggested that climate change and historical forest management contributed equally to the recent outbreak intensification in Europe.

Although bark beetle outbreaks have been intensifying in Europe for more than two decades (Seidl et al., 2014), the size of the very recent spruce mortality pulse was unprecedented (Senf et al., 2020; Schuldt et al., 2020). This outbreak eruption was observed in several countries, including Austria, Germany, and France (e.g. Jandl, 2020; Senf and Seidl, 2020; Sommerfeld et al., 2020), with the Czech Republic becoming an epicenter (Hlásny et al., 2019; Toth et al., 2020). The most recent outbreak in the Czech Republic started in ca. 2015 and exceeded ranges observed over the last two centuries. The outbreak received various connotations such as the ecological collapse or failure of spruce-oriented management. Large pulses of salvaged timber had overarching effects on the regional forest-based sector and raised a great interest among the public, ecologists, timber industry experts and policy-makers in understanding outbreak mechanisms and prospects. Understanding recent changes in disturbance regimes is also important for developing management strategies that are able to address the emergent ecosystem dynamics, such as resilience-oriented stewardship (Senf and Seidl, 2020).

In response to these challenges, we aimed to investigate here the spatial and temporal dynamics of bark beetles in the Czech Republic during the last 20 years, focusing particularly on the period 2017–2019, which was characterized by an unprecedented outbreak intensity. With regard to the cascade of impacts triggered by the outbreak, we further aimed to understand major implications on forest owners, the environment, and the society and how different actors responded to the outbreak and its management. We hypothesized that the outbreak was triggered by the extremely dry climate in recent years, which replaced the role of wind as the notorious outbreak trigger in Central Europe. We further hypothesize that the outbreak triggered a cascade of processes involving different sectors and social groups, resulting in tensions that constrained management efforts. Such an investigation can help one to better understand the broader social context of the outbreak and inform future management decisions.

2. Data and methods

2.1. Forests and forestry in the Czech Republic

The Czech Republic belongs to the temperate forest zone of Europe with a temperate oceanic climate (Rivas-Martínez et al., 2004). Forests cover 2.67 million ha, representing 34.1% of the land area. Intensive management applied over the last three centuries resulted in the dominance of Norway spruce that represents 50% of the current tree species composition. Scots pine *Pinus sylvestris* (16.2%) and European larch *Larix decidua* (3.8%) are other abundant conifers. Broadleaves constitute 27.3% of the species composition, with dominance of the European beech *Fagus sylvatica* and oaks *Quercus* sp. Both dominating conifers, spruce and pine, have been suffering from mass mortality due to drought and biotic attacks in recent years. Forests under the state ownership represent 55% of the total forest area, while the non-state forests (private, church, and municipal) are owned by ca 300,000 different legal entities. Small-scale clear-cutting (1 ha area) with a mean forest rotation age of 115 prevails (Ministry of Agriculture of the Czech Republic, 2019).

2.2. Studied disturbance system

The investigated outbreak was caused by the European spruce bark beetle *Ips typographus* (L), which is the main biotic disturbance agent in Norway spruce forests in Eurasia (Biedermann et al., 2019). *I. typographus* attacks spruce trees to access fresh phloem needed for brood development. Successful colonization is typically fatal to trees, because beetles destroy the inner bark and thus disrupt nutrient transport to roots. *I. typographus* causes intermittent outbreaks with devastating effect on forest landscapes, which are typically interrupted by long non-outbreak periods (Raffa et al., 2008). In the non-outbreak period when beetle populations are small, beetles avoid tree defense by entering only freshly dead or stressed trees (Huang et al., 2019). During the outbreaks, however, bark beetles can exhaust tree defense by mass coordinated attacks. While factors triggering the outbreak are relatively well understood, factors leading to outbreak collapse are subject of scientific debate (e.g. Biedermann et al., 2019).

In Central Europe, population transition to the outbreak phase is typically triggered by windthrows, which provide large amounts of breeding substrate (Mezei et al., 2017; Stadelmann et al., 2014). Notorious outbreak areas where wind and bark beetles represent a typical disturbance regime are, for example, the Bavarian Forest in Germany (van der Knaap et al., 2020), the High Tatras in Slovakia (Mezei et al., 2017), and the Bohemian Forest in Czechia (Zemek et al., 2003). Outbreaks can also be triggered by other factors compromising tree defense, particularly hot and dry weather (Marini et al., 2017; Netherer et al., 2019).

I. typographus exhibits large phenological plasticity in thermally-regulated traits and this allows it to adjust the number of annual generations and generation timing to local climates (Bentz et al., 2019). A warming climate therefore not only compromises tree vitality and defense, but it also reduces the winter mortality of beetles and allows the completion of additional beetle generations per year (Baier et al., 2007; Berec et al., 2013). Recent observations from the Czech Republic indicate a shift to a three-generation regime in some locations, likely contributing to the recent increase in tree mortality.

Bark beetle management follows two major objectives, i.e. outbreak prevention and outbreak containment (Wermelinger, 2004). While prevention mainly aims at keeping beetle densities low via sanitation removal of infested trees, beetle trapping, application of pesticides, and the swift removal of wind-felled trees, containment mainly aims at massive salvage and sanitation logging in outbreak areas or their surroundings to prevent outbreak expansion (Faccoli and Stergulc, 2008; Holuša et al., 2017). The efficiency of these strategies, however, has recently been increasingly questioned (Dobor et al., 2020b, 2019; Hlásny et al., 2019).

2.3. Data

To characterize spatial and temporal dynamics of bark beetle disturbance, we combined several sources of data on forest damages reported by forest owners. First, we used annual reports of the Czech Forest Protection Service (FPS) from the period 2003–2019. The reports include amounts of salvaged trees (m^3) killed by different agents. Strict legal obligation to salvage dead trees suggests a high correspondence of killed and salvaged trees, yet the salvaging rate may change depending on local circumstances. We extracted "bark borers on spruce" category from the FPS statistics. Vast majority of killed trees in this category accounts for *I. typographus,* though other species such as *I. duplicatus, I. amitinus* and *Pityogenes chalcographus* can be locally important (Holuša et al., 2012, 2010). The data are reported for administrative districts at the LAU1 level of the EU nomenclature (Local Administrative Units, n = 77). These reports are mainly based on data reported by the Forest of the Czech Republic and the Military Forests and Properties, and cover ca 70% of the total forest area of the country. The completeness of the data (i.e. part of the total forest area covered by the source reports from forest owners), however, varies between years.

Second, we used annual reports of the Czech Statistical Office (CSO), which contain forest damage records reported by all economically active entities in the Czech Republic at the level of NUTS3 (Nomenclature of Units for Territorial Statistics, EUROSTAT, n = 14). Therefore, while spatial resolution of these data is lower than that of the FPS data, they cover a larger forest area. Consistently with the FPS data, we extracted annual data on bark-beetle-related salvage logging for the period 2003–2019 from the CSO statistics.

Both data sources (FPS and CSO) are derived by aggregating primary data reported by forest owners. The source units of the reporting are rather heterogeneous, depending on the ownership structure, and are not consistent with the boundaries of administrative districts. The primary source data, however, are not publicly available.

Next, we combined the two data sources to create a dataset with coverage of CSO, and the resolution of FPS. First, we summed salvaged volumes in LAU1 districts (FPS) pertaining to each NUTS3 district (CSO), yielding 14 pairs of salvaged volumes for each year ($\Sigma LAU1_{ij}$ vs. $NUTS3_j$, where i = 1–77 (LAU1) and j = 1–14 (NUTS3)). The ratios of these value pairs yielded a set of coefficients, which were applied on the LAU1 salvaged volumes to ensure that they reached the levels of the CSO statistics. Such a procedure preserved the spatial pattern of salvaged volumes reported by the FPS (LAU1 level), while matching the sums of salvaged volumes in the CSO data (NUTS3 level).

To reach a more realistic allocation of differences between LAU1 districts pertaining to the specific NUTS3 district, we calculated the proportions of spruce in species composition in each LAU1 relative to the spruce growing stock in the respective NUTS3 (Source: Forest Management Institute of the Czech Republic), and redistributed the respective differences accordingly. Hence, the total salvaged volumes from the CSO statistics were preserved, and the distribution of values across the LAU1 districts was refined by considering the actual distribution of Norway spruce. The final dataset that was subject to further analyses consisted of 77 times series (2003–2019) associated with the 77 LAU1 districts.

The third source of data used was data on actual spruce growing stock in all years of the study period. These data were extracted from the Forest Management Plan (FMP) database supervised by the Forest Management Institute of the Czech Republic. The data are being updated in the field in a 10-year cycle, so they are not temporally consistent with the previously described annual damage data. We therefore modified the growing stock by salvaged volumes on an annual basis, with regard to the year when the FMP data for the largest forest area within an LAU1 district were updated. This modification was particularly important in districts where the outbreak has recently culminated, and spruce growing stock was reduced within a short period of time. We also adjusted the actual growing stock levels by the estimated volume increment and regular harvests. Here we note that regular harvests have been substantially reduced during the recent outbreak period (2018–2019) to mitigate impacts on the timber market (Toth et al., 2020).

Climate data were derived from weather stations supervised by the Czech Hydrometeorological Institute. Data quality control and homogenization were conducted based on the methods described by Štěpánek et al. (2013). Source daily values were aggregated into monthly, seasonal and annual means (air temperature) or sums (precipitation). The monthly aggregates were interpolated by means of the regression kriging into the maps with a spatial resolution of 500 m. Various terrain characteristics were used as predictors in the interpolation. The monthly maps were then used to calculate different annual statistics to be used as predictors in the developed regression models (Appendix A) for all districts (n = 77). The Standardized Precipitation-Evapotranspiration Index (SPEI) was calculated based on the method described by Vicente-Serrano et al. (2010) and Beguería et al. (2014). The calculation was conducted using the R package SPEI (Vicente-Serrano et al., 2010) and ProClimDB software (Štěpánek, 2010).

2.4. Regression modelling design and data

To identify the drivers of bark beetle dynamics over the period 2003–2019, we formulated a statistical model based on the Generalized Additive Models (GAMs) (Wood, 2017). GAMs are used for modelling complex regression functions and gained an increased recognition in ecological research (Pedersen et al., 2019). GAMs approximate the relationship between the response variable and the predictors by means of several non-linear smooth functions, which are subject to inferences and interpretations. GAM fitting aims to determine the optimal smoothing parameters, while controlling for the model's overfitting. GAMs are formally defined as:

$$g(E(Y)) = \alpha + s_1(x_i) + \ldots + s_p(x_p)$$

where Y is the response variable, $E(Y)$ is the expected value, and $g(Y)$ is the link function that links the $E(Y)$ to the predictor variables $x_i, \ldots, x_p$. The terms $s_i, \ldots, s_p$ are nonparametric smooth functions.

The first response variable used was the percent of spruce growing stock annually affected by bark beetles and salvaged (Kill%) in each year of the period 2004–2019. The number of records used to estimate the model parameters was given as 77 LAU1 districts × 16 years (2004–2019; the year 2003 was omitted to allow for including predictor variables shifted by one year backward, such as the wind-felled volumes from the previous year). Second, we investigated Kill% over the recent period 2017–2019, when the level of disturbance culminated (Fig. 1) (i.e. three years × 77 districts). Third, we investigated the slope of the linear regression of Kill% over the period 2017–2019 (Slope; one value × 77 districts) (Appendix A). In the latter case, we considered forest and climate conditions from the year 2018 as predictors.

The candidate predictor variables included the long-term annual mean temperature and precipitation total characterizing the position of districts along the major climatic gradients in the country, the mean forest age and proportion of spruce in the districts, the volume of salvaged wind-felled trees, the annual temperature and precipitation anomalies (difference from the long-term average 1980–2010), and the annual Standardized Precipitation-Evapotranspiration Index (SPEI; Thornthwaite, 1948)) (Appendix A). The volume of salvaged windfelled trees needs to be interpreted as the relative intensity of wind disturbance rather than the availability of breeding substrate, as it represents the amount of removed rather than retained windfelled trees. In case of windfelled volumes and annual climatic predictors, we considered values from both the actual and the preceding year. We used a step-wise selection to identify the predictors to be included in the model.

The Kill% was modelled using a Tweedie distribution (Wood et al., 2016) with the log link function. The Slope was modelled using a Gaussian distribution with the log-link function. A thin plate regression spline was fit to each predictor variable. Selected interactions between the predictors based on the tensor product approach were included in the models, too.

We constructed several statistical models and tested their performance using the Akaike Information Criterion, by evaluating the statistical properties of residuals, and the amount deviance explained (analogous to variance in a linear regression) by the models. We used R library mgcv (Wood, 2017) to conduct the presented analyses.

2.5. The Pettitt test

We used the Pettitt test (Pettitt, 1979) to identify years where Kill% started to increase in the LAU3 districts. The Pettitt test is a non-parametric test that identifies change points (years of significant change in time series of Kill% in this study) in a univariate time series based on the Mann-Whitney statistic. We used the R package trend v.1.1.2. for this analysis (Pohlert, 2020).

3. Results

3.1. Spatial and temporal patterns

Total volume of trees killed by bark beetles and salvaged across the Czech Republic oscillated around 1.5 million m^3 annually in the period 2003–2015, representing 0.2% of the total growing stock (Fig. 1a). Years 2015 and 2016 exhibited substantial increases in the disturbance rate, reaching 2 and 4 million m^3 annually, respectively. Most dramatic increase occurred in 2018, reaching 13 million m^3. In 2019, the amount of salvaged trees killed by bark beetles increased further, reaching nearly 23 million m^3 (3.2% of the total growing stock). Spruce growing stock decreased from 511 ± 15 mill. m^3 in 2011–2014 to 430 ± 15 million m^3 in 2019 (−16%) (Adolt et al., 2020).

While trees killed by bark beetles represented 10–49% of the total salvaged volume in the period before 2018, they dominated in the period 2018–2019, accounting for 56–73% of the salvaged stock (Fig. 1a). At the same time, while salvaged volume due to bark beetle attacks represented 5–30% of the total harvests before 2018 (i.e. salvaged and planned), it accounted for 50–70% in 2018–2019. Moreover, total salvaged volume (caused by all disturbance agents) in 2018–2019 represented 90–95% of the total harvests; i.e. planned harvests were greatly reduced for logistic and market reasons.

Kill% started to increase in most of the districts in 2014, while the increase was delayed in several districts in the western part of the country by 2–3 years (Fig. 1bd). Decreasing Kill% in the period 2017–2019 was observed only in four districts in the north-east (Fig. 2), where the outbreak that has persisted there since the 1990s (Hlásny and Sitková, 2010) already depleted spruce stocks, resulting in the opposite trend to the rest of the country.

Bark beetle disturbance was scattered across the country before 2017, remaining below 0.5% of the growing stock affected (and salvaged) annually (Fig. 2). The outbreak expanded dramatically in 2018–2019, culminating in the southeastern districts. The highest acceleration of the outbreak indicated by the slope of linear regression in Kill% over the years 2017–2019 was observed in the south-eastern districts too.

The outbreak has not yet affected the high-elevation areas in the northwest of the country with a high spruce proportion (grey areas in Fig. 2). These districts were severely affected by air pollution in the 1970s and 1980s, shifting forest age structure towards younger and less vulnerable stages. Moreover, these areas are characterized by a colder and wetter climate than most of the remaining districts. In particular, long-term (1980–2010) average annual precipitation total in districts depicted in grey in Fig. 2 was 775 mm, while it was 670 mm in the rest of the country. The same comparison for temperature is 7.3 °C vs. 8.1 °C.

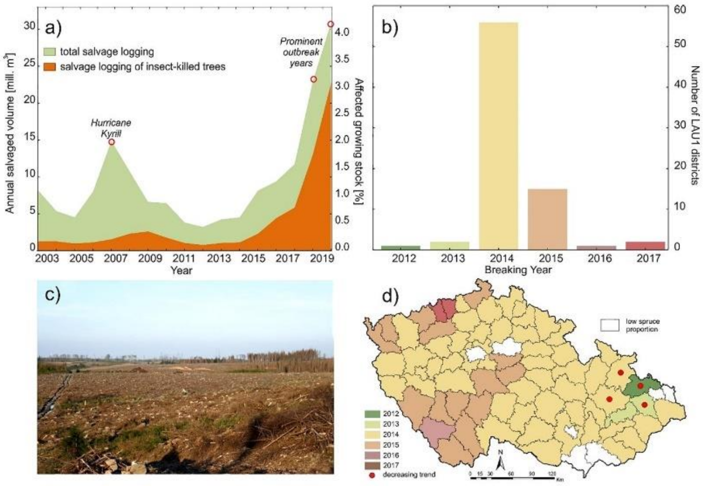

Fig. 1. a) Total annual salvaged volume and salvaged volume of trees killed by bark beetles in the Czech Republic over the period 2003–2019 (left axis). The right axis shows an approximate percentage of affected growing stock. Major disturbance events are indicated too. b) Distribution of years with a significant change in the times series of Kill% in the districts of the Czech Republic as indicated by the Pettitt test. c) A post-outbreak salvaged area (North-eastern Czechia, the Olomouc county). d) Spatial distribution of the years of significant change in time series indicated in the panel b). Red dots indicate districts where the disturbance rate decreased after the year of significant change. White areas indicate districts with low spruce proportion, which were excluded from the investigation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

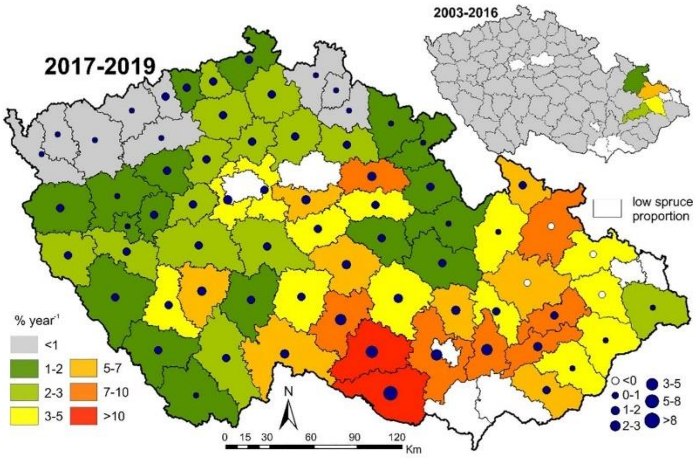

Fig. 2. Average percent of spruce growing stock affected by bark beetles and salvaged over the period 2017–2019. The circular symbols show the slope of the linear regression over this period. The insert map shows the situation in the preceding period 2003–2016.

3.2. *Drivers of bark beetle dynamics*

3.2.1. *Longer-term perspective*

We retained in the analysis of bark beetle dynamics in the period 2004–2019 the following predictor variables: the mean annual air temperature in the period 1980–2010 (T), the proportion of spruce (Spruce%), the mean spruce age (Age), the amount of windfelled and salvaged wood in the preceding year ($Wind_{-1}$), the temperature anomaly (Tanom), and the Standardized Precipitation Evapotranspiration Index (SPEI) (Appendix A). The data represent average values for the LAU1 districts ($n = 77$). Moreover, we included the interaction term Spruce% × Age. The model explained 73% of deviance of Kill%. All of the predictors except for Age were found to have a smoothing term significantly different from zero ($p < 0.001$). We, however, also retained the Age variable as its interaction with Spruce% was significant, and markedly increased the amount of explained deviance (Fig. 3).

Response of Kill% to T had a U-shaped pattern, indicating that bark beetles were affecting forests across a broad range of temperature

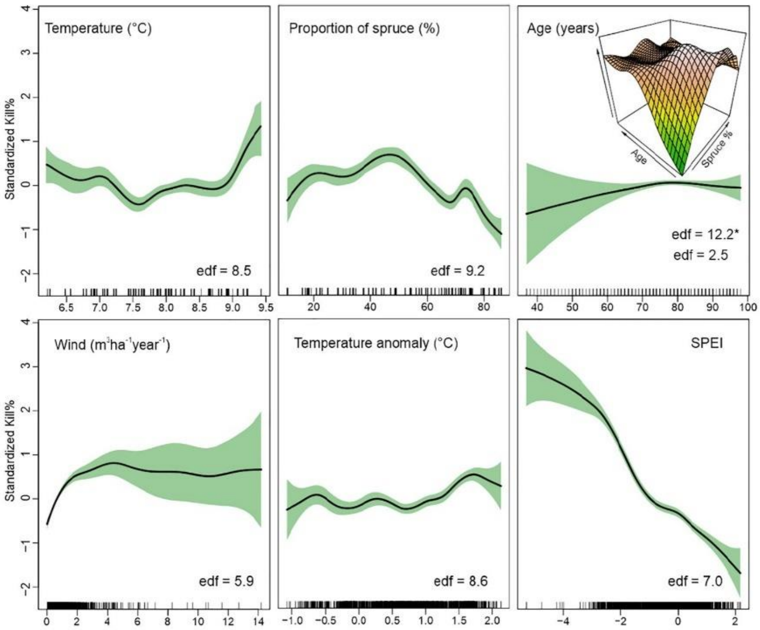

Fig. 3. Response of Kill% in the 77 districts of the Czech Republic in the period 2004–2019 to selected predictors modelled by means of the Generalized Additive Models. A 95% confidence interval is indicated for each smooth term. The insert in the Age panel indicates the interaction of Spruce % and Age. Marks along the horizontal axis represent single observations. edf – effective degrees of freedom. *indicates edf for the interaction term. SPEI – Standardized Precipitation-Evapotranspiration Index.

conditions. Still, there is an increased level of disturbance in districts with the mean annual air temperature above 9 °C. A unimodal response to Spruce% culminating at 50% proportion of spruce in the districts reflects the fact that the districts with high spruce proportions located mostly in the western part of the country have not yet been affected by bark beetles. The response of Kill% to Age was indistinct, though slightly increasing with an increasing age. Kill% increased in response to wind disturbance intensity (approximated by the volume of salvaged windfelled trees) from the previous year (Wind$_{-1}$). This increase was distinct at low levels of wind impact, whereas it remained stable under higher windthrow intensities. Response of Kill% to Tanom was indistinct up to the value of +1.5 °C, and then increased. The response of Kill% to SPEI was found to be most distinct. Low SPEI values indicating reduced water availability correspond with the highest levels of Kill% and vice versa. The lowest values of SPEI and the highest values of Tanom correspond with the period of recent outbreak intensification from 2018 to 2019 (Appendix B).

3.2.2. Perspective of the recent outbreak culmination

Further, we investigated the drivers of Kill% in the outbreak period 2018–2019, and the drivers of outbreak acceleration over the period 2017–2019 as indicated by the slope of the linear regression of Kill% (Slope) (Fig. 4). The models explained 64% and 66% of deviance in Kill% and Slope, respectively. Both Kill% and Slope were positively associated with warmer (T) and drier conditions (SPEI). Kill% was affected by forest age, while the outbreak accelerated more intensively in districts with a higher spruce proportion. Interestingly, Age did not affect Slope and Spruce% did not affect Kill%. Finally, higher levels of Kill% were associated with districts experiencing an excess of precipitation (Panom), a relationship lacking an ecological interpretation. Wind-related variables did not have any effect on either response variable in this recent period.

3.3. Outbreak impacts and responses

The outbreak and extensive counter-measures triggered a cascade of processes affecting different sectors and social groups. We evaluated a large number of media articles, annual reports of state administration, forest enterprises and NGOs to identify four broad categories of impacts, which required different responses from the state administration and forest management (Table 1).

A number of sources have indicated negative impacts on the quality of life and the safety of inhabitants in the affected areas. These impacts included a risk of injuries from falling trees and forest mechanisms as well as the heavy traffic of trucks with salvaged timber, damage to the roads and an increased risk of traffic accidents. The outbreak reduced forest recreation and scenic values over an area of up to ca. 55,000 ha, including ca. 13,000 ha of protected areas (national parks, protected landscapes, etc.). Measures taken to mitigate these impacts included communication campaigns, an extensive clearing and reforestation of disturbed areas, investments into roads reconstruction, and the adoption of new regulations harmonizing the need of excessive transportation with impacts on the quality of life of affected inhabitants (see Table 1).

Economic implications of the outbreak were mainly related to the excessive workload related to the salvaging and reforestation of cleared areas as well as the decrease in timber price (Table 1, Appendix D), causing an economic decline of many forest owners and enterprises. Alleviating these impacts required state interventions in terms of subsidy, compensation and recovery payments amounting for ca. 260 million EUR in the period 2018–2019. The estimated amount of these payments for 2021 is 267 million EUR (Ministry of Agriculture of the Czech Republic, 2020, 2019).

The effect of management on areas under different level of protection was identified as another important outbreak implication. The management included a heavy salvaging of dead trees and the use of insecticides in storage yards, and it often did not respect processes such as

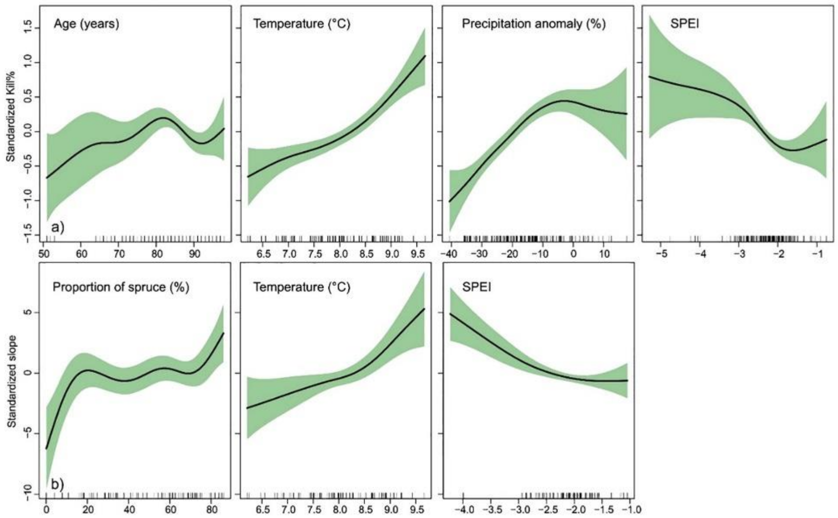

Fig. 4. Response of a) Kill% in the period 2018–2019 and b) the slope of the linear regression of Kill% to the main predictors over the period 2017–2019.

Table 1
Overview of impacts generated by the outbreak and its management, and measures taken to alleviate these effects.

Type of impact	Specific process	Quantifiable effects	Measures taken
Social and economic impacts	Reduced forest scenic and recreational values	Size of cleared areas increased from 19,000–25,000 ha (2004–2015) to 34,000 and 55,000 ha in 2018 and 2019, respectively	Reforestation applied over the area of 21,000 and 27,000 ha in 2018 and 2019, respectively; Regeneration and tending subsidized
	Restricted access to the forest	—	Salvaging applied along hiking trails to reduce the risk of injuries; Reconstruction of hiking trails
	Damage to roads by the excessive transportation of salvaged timber	At least 400 km of roads damaged	State intervention of 160 million EUR planned for 2021; Max. permissible lorry weight reduced
	Reduced quality of life of inhabitants by a high-frequency transportation of salvaged timber; risk of traffic accidents and jams	—	Communication campaigns by the Ministry of Agriculture
	Revenue loss due to the high investments into salvage harvesting, decrease in timber price, increased expenses related to the regeneration of cleared areas, and other cascading effects	Spruce log price decreased from 84 to 57 EUR between 2017 and 2019; Size of areas to be reforested increased up to 55 000 ha; Major state forest enterprise in negative balance (-30 mill. Euro in 2019); (see Appendix D for selected indicators)	Subsidy, compensation and recovery payments amounting for 259 million EUR in 2018–2019; 267 million EUR allocated for 2021
Conflicts with natureconservation	Increased use of insecticides with potential risk for the environment	The use of insecticides increased almost fourfold during the period 2017–2020, and use of alpha-cypermethrin coated nets* almost sevenfold (Forests of the Czech Republic, pers. comm.).	Recommendations on outbreak management in different protected areas (including Natura2000 sites) by the Ministry of Environment; Improved management guidelines by natural park administrations; Management recommendations by NGOs; No new legally binding regulations adopted with regard to the outbreak
	Damage to nature conservations areas from bark beetles and management activities	13,000 ha of the protected areas were affected by the outbreak (AOPK ČR, 2020)	
	Conflict about the fate of standing dead trees with no effect on bark beetle populations and low economic value	6 million and 5–10 million m^3 of dead andinfested trees remained in the forest in 2018 and 2019, respectively	
	Habitat destruction, disturbing reproduction of species of conservation concern (e.g. woodpecker *Dryocopus martius*, black grouse *Tetrao tetrix*)	—	
Tension between post-outbreak reforestation and game management	Subsidized planting of seedlings on cleared areas is countered by high-intensity game browsing. High game populations are advocated by some hunting associations and other interest groups.	Approximate cost of damages from browsing 1 million EUR annually (Ministry of Agriculture of the Czech Republic, 2019); almost total devastation of non-spruce species in regeneration	Hunting season for all regeneration damaging game species extended to the whole year; Regeneration protection (repellents, fencing) subsidized; Establishment of shooting corridors in reforested areas; Motivation payments for hunters
Depletion of logistic and human resources	Management is constrained by bottlenecks in transportation and storage of salvaged wood, and production of seedlings in nurseries	1,500 railway wagons missing in 2018	Establishment of new storages for salvaged wood; Wood storage on agriculture land allowed; Enhancing railway transport capacities; Reduction of planned harvests; Nurseries adjusting their production to the new demands, millions of spruce seedlings destroyed and replaced; Relaxed roles for the geographical transfer of reproductive material; Extended reforestation period
	Excessive workload, lack of available workforce and restricted mobility of seasonal workers due to the COVID crises caused increase in labour price and lack of forestry workers	An estimated shortage of ca 6,000–10,000 forest workers annually	Simplified visa procedure for the Ukrainian workers

* A fabric net coated by an insecticide and used to cover the infested logs to prevent the beetles from leaving them (e.g. Skrzecz et al., 2015).

bird nesting (see Table 1 for quantitative indicators) (AOPK ČR, 2020). As a response, different state and non-governmental nature conservation organization developed recommendations and management guidelines on mitigating the adverse effects (e.g., Ministry of the Enviroment of the Czech Republic, 2019). However, no legally binding regulations beyond the scope of the existing legislation were adopted in this regard.

Another issue of critical importance concerned the devastating effect of game on forest regeneration. Investments into the planting of desired tree species on cleared areas were, in fact, cancelled out by high-intensity browsing. Systematic game reduction was, however, opposed by different interest groups. The estimated damage was found to amount for ca. 1 million EUR annually (Ministry of Agriculture of the Czech Republic, 2019). This required the adoption of unprecedented measures such as the extension of hunting season over the whole year, the establishment of shooting corridors in the reforested areas, and payments to hunters (Table 1).

The final outbreak implication included the fast depletion of logistic and human resources. Except for depleted storage and transportation capacities, up to 10,000 forest workers were estimated to be missing annually. The measures taken included relaxed visa procedures for foreign workers, a country-wide survey of places serving as storage yards, and an increase in railway transport capacity (see Table 1).

4. Discussion

Bark beetle disturbances are increasing globally, yet some aspects of such dynamics as well as the social, market and ecological implications remain insufficiently understood (Morris et al., 2017). We investigated here the most recent outbreak of bark beetles in the Czech Republic that has exceeded ranges of disturbance impacts recorded in the managed forests of Central Europe over the past two centuries. We found a transition from wind- to drought-driven outbreak dynamics as well as a transition from mostly locally manifested outbreaks to the regional and supranational dynamics. Our findings highlighted a low level of social preparedness to face the outbreaks (or natural disturbances in general) amplified by climate change and questioned the sustainability of production forestry oriented on Norway spruce that is broadly practiced in Central Europe. We discuss here the underlying mechanisms of the investigated outbreak dynamics, management implications, and identify the pathways of future research.

4.1. Outbreak dynamics

Most of the previous outbreaks of bark beetles in Central Europe were triggered by windthrows and occurred in geographically isolated areas (Hlásny and Turčáni, 2013; Lausch et al., 2013; Mezei et al., 2017; Modlinger and Novotný, 2015), though they were likely synchronized by climate variation and other factors acting on a large scale (Økland et al., 2005; Senf and Seidl, 2018). The ongoing outbreak deviates from this dynamic by its size and that it was not associated with any significant windthrow. Our analysis supported this observation, i.e. while the effect of wind was significant in the entire period 2003–2019, this was not the case in the recent outbreak period 2017–2019. Our findings instead suggested the prominent role of drought in unfolding large-scale epidemics. Such dynamics were described by Marini et al. (2017), who suggested that drought and climate warming can boost population eruptions even in the absence of windthrows. While these authors found no synergies between outbreak drivers, other studies found a strong amplifying effect of wind and warmer and drier climate on bark beetle dynamics (Dobor et al., 2020a, 2020b; Seidl et al., 2017). Such interactions deserve attention in future research as they may form a new disturbance dynamic in Central Europe. For example, outbreaks may be triggered by drought in hot and warm years (i.e. the incidence of a windthrow may not be a necessary precondition of the outbreak), whereas wind can trigger population transitions in cooler and moister years, cumulatively resulting in increased disturbance levels. Still, there are indications that outbreaks triggered by drought, though of a smaller extent, occurred in Central Europe also in the past (e.g., Zahradník and Zahradníková, 2019).

We found that the level of killed trees started to increase in 2014 in most of the country, and the outbreak accelerated in the remarkably dry year of 2015. Another critical acceleration corresponded with the climatically extreme year of 2018. The 2015 drought (along with the year 2003) represents the most intense drought initiated during the vegetation period over the previous 250 (Hanel et al., 2018) or 500 years (Orth et al., 2016). The 2018 drought even exceeded the severity of previous events (Schuldt et al., 2020). The 2018 increase in outbreak intensity corresponds with the fact that the highest canopy mortality over the past 34 years in Europe was observed in 2018 (Senf et al., 2020), though bark beetles represented just one factor driving this dynamic. All these events had drastic impacts on the European ecosystems, exceeding the limits for xylem hydraulic failure in many species, widespread discoloration, and premature leaf shedding (Bastos et al., 2020a, 2020b; Schuldt et al., 2020). In spruce, these events likely compromised resin exudation and the overall defense capability against bark beetles (Netherer et al., 2015), resulting in the observed outbreak accelerations. It remains unclear why bark beetle disturbance did not increase in response to the 2003 drought that particularly affected the western part of the Czech Republic (Hanel et al., 2018), while this event led to extensive forest damage across Europe (Rouault et al., 2006).

Another factor contributing to the severity and size of the outbreak was the unfavorable structure of the Czech forests that was particularly conducive to large-scale outbreaks. Norway spruce represents 52% of species composition in the country and occurs mostly in monocultures, and vulnerable age classes prevail (Podrázský et al., 2014). Most of the spruce forests are distributed in low to medium elevations, where the risk of drought stress is high, and two to three bark beetle generations can be produced annually (Berec et al., 2013; Hlásny et al., 2011). Spruce also cannot exploit the potential buffering effect of topographic complexity in such environment (Albrich et al., 2020). At such sites, the risk of spruce damage is sevenfold higher than in its historical range (Marini et al., 2012). Moreover, spruce planted in monocultures has a significantly lower survival probability than spruce growing in species diverse stands (Griess et al., 2012; Neuner et al., 2015). Our analysis of outbreak drivers is consistent with these findings, highlighting the importance of forest age, spruce share, and air temperature as predisposing factors of infestation.

A further outbreak development remains unclear, particularly due to the importance of hardly predictable climate extremes as well as insufficient understanding of mechanisms causing outbreak collapse (Biedermann et al., 2019). Still, that the remaining spruce growing stock amounts to ca. 400 million m^3 makes outbreak collapse due to the resource depletion unlikely. Instead, the current outbreak's epicenter may shift westwards after the resources are depleted, or the outbreak may expand. Moreover, climate projections consistently predict the increase in climate extremes, including drought (Grillakis, 2019). Therefore, outbreak collapse due to the persistently colder and moister climate is unlikely too. High rates of disturbance thus should be expected to persist in the coming years or decades, though weather-dependent inter-annual variation can be large.

We suggest that the coincidence of extreme climate with unfavorable forest conditions pushed the regional spruce forests to the margins of their operational space (see e.g. Keane et al., 2009; Turner et al., 2020). The current outbreak can thus be thought of as the beginning of a large-scale transformation of secondary spruce forest to other forest types, with a better match to the emergent environmental conditions. For example, Albrich et al. (2020) found in the Eastern Alps that a warming above 2 °C can trigger a shift from a conifer-dominated landscape characterized by large trees to a landscape dominated by smaller, predominantly broadleaved trees. These considerations underscore the utility of resilience framework (Johnstone et al., 2016; Scheffer et al., 2009; Turner et al., 2020) in understanding the ongoing changes in the Central European forests and their future developments.

4.2. Social and multi-actor implications

Because no systematic research on outbreak impacts existed at the time of this study, we relied on numerous public materials published by state administration, NGOs, and other bodies (e.g. Takala et al., 2019). Although such data cannot replace a sound social and economic analysis (e.g., Montagné-Huck and Brunette, 2018; Qin and Flint, 2010), they represent a sensible estimate of outbreak implications. Such an analysis can also serve as a baseline for the next assessments, helping to understand the temporal evolution of impacts and responses, which can be vital for informing future management strategies (Qin and Flint, 2010).

We found that the outbreak generated new interactions between forest management on the one side, and labor market, transportation, game management and nature conservation on the other. Most of these interactions had a negative connotation and were constraining management decisions. Such a situation partly stems from the long-term lack of participatory approaches in forestry decision-making (Hoogstra-Klein et al., 2017) and poor harmonization of sectoral policies (Fürst et al., 2017). We identified the tension between forest management and nature conservation to be particularly disturbing. Although efforts to resolve this tension is a notorious part of the public discourse and political agenda (Maier and Winkel, 2017; Mikusiński et al., 2018), the ongoing outbreak showed that the current policies are not aligned to the emergent large-scale disturbances. Some aspects of this situation resemble the case of the Białowieża Forest Massif in Poland (Blicharska et al., 2020), where efforts to control bark beetle outbreak were not found to be aligned with local conservation objectives and EU legislation.

In this study we primarily focused on the prevalent adverse effects of the outbreak and measures taken to mitigate them. Such a picture is however, incomplete, as the outbreak has also initiated positive societal processes. For example, the loss of mature trees and related cultural services increased public awareness of the societal role of the forests and highlighted the prominence of forest adaptation to climate change. Such a tendency was evidenced by an increase in the frequency of the word *bark beetle* (in Czech) on the Internet from 7 to 30,000 annually over the period 2000–2016 to 50,000–135,000 over the period 2018–2020 (Appendix C). The outbreak also increased the involvement of the scientific community in advising the formulation of forestry policies, and promoted public involvement and volunteering (e.g. in planting the seedlings on disturbed sites). The outbreak has accelerated the transformation of forestry legislation towards increased preparedness, capacity building and better harmonization of forestry and nature conservation policies. Therefore, instant negative effects reported in this study need to be considered along with the positive effects, though their lead times can be long (e.g., the effects of increased awareness).

4.3. Management perspective

The investigated outbreak has challenged forest management by its size and rapid expansion that exceeded logistic and human resources. The bottlenecks identified throughout the entire processing chain along with the previously described multi-actor interactions define boundaries that constrain management decisions. The two major tasks that are being addressed in the context of these constraints are: (i) how to slow the outbreak down and mitigate impacts on forest owners and the entire forest-based sector, and (ii) how to regenerate the outbreak areas towards their climate adaptedness and resilience. Obviously, these short-term and forward-looking objectives compete for limited resources, and priorities differ between the stakeholders (forest owners, state administrations, timber industry vs. nature conservation, and a part of the public). The most undesired consequence of this situation would be the emergence of a new, even-aged forest cohort dominated by spruce with low resilience to future disturbances. Although a warmer climate disfavors spruce in regeneration, factors such as spruce dominance in the existing seed bank and the advanced regeneration, and the availability of spruce seedlings on the market rather than seedlings of other species (though nurseries are quickly adapting to the new demands), may compromise the resilience of the future forest (e.g., Zeppenfeld et al., 2015). Management should therefore harmonize the reforestation of cleared areas with the natural changes in the regeneration driven by climate change, reaching a higher share of climate-matching tree species in the new forest cohort (Bolte et al., 2010; Vacek et al., 2019).

The size of the outbreak investigated here highlighted the importance of a multi-scale perspective in forest management, addressing, for example, the connectivity of spruce complexes in order to prevent the large-scale spread of bark beetles (Seidl et al., 2013; Simard et al., 2012). Because a landscape-scale forest configuration is an important driver of forest resilience (Seidl et al., 2016b), neglecting this scale in outbreak management as well as the follow-up recovery actions may result in a low resilience of future forests. However, the adoption of the landscape perspective is typically hampered by factors such as fragmented forest ownership, a poor coordination among forest owners, and a traditional focus of Central European forestry on the stand-scale (Jactel et al., 2009; Seidl et al., 2016a). The second aspect we highlight here is that the dampening effect of sanitation removal of infested trees on bark beetle dynamics was found to strongly diminish under warmer and drier climate (Dobor et al., 2020a, 2020b, 2019). This is a disturbing fact because search for and removal of infested trees aiming to control the outbreak are heavily conducted. We therefore suggest that actions aiming at the proper regeneration of post-outbreak sites and preventative measures in areas that have not yet been affected (e.g., premature harvesting, the preventative sanitation removal of infested trees, etc.) should be preferred over actions aiming at outbreak suppression in the major outbreak areas. These facts indicate that a shift of the management paradigm towards landscape-scale considerations and resilience-oriented stewardship is needed if the outbreak occurs on a large-scale and is fueled by climate change.

5. Conclusions

The Czech Republic has become an epicentre of bark beetle outbreaks that devastate Europe's forests. Our investigation showed that the current outbreak synchronously affected areas of an unprecedented size and was predominantly driven by drought, which is a new phenomenon in Central European forests. As the frequency and severity of droughts will continue to increase, such a situation is likely to occur also in the future, though the dynamics of this development remains unclear. We further showed that the outbreak has challenged all aspects of forest management and its impacts extended far beyond forestry. Negative social responses and emergent tensions between the different actors constrained forest management and required state interventions, including subsidy and recovery payments as well as changes in legislation. We suggest that although this study was conducted in the Czech Republic, it likely characterizes processes occurring at much larger territories in Central Europe and can also inform the management of disturbances other than bark beetles.

CRediT authorship contribution statement

T. Hlásny: Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Formal analysis. **S. Zimová:** Resources, Data curation, Formal analysis. **K. Merganičová:** Resources, Data curation, Writing - review & editing, Formal analysis. **P. Štěpánek:** Resources, Data curation, Software. **R. Modlinger:** Resources, Data curation, Writing - review & editing. **M. Turčáni:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Variables investigated using the GAM-based regression modelling

See Table A1

Table A1
Response and candidate predictor variables used to investigate the drivers bark beetle dynamics in the Czech Republic.

Variable set	Variable abbreviation	Variable	Avg ± St. Dev.	Min	Max
Response variables	% Killed (2003–2019)	Percent of total growing stock killed by bark beetles (%)	1.35 ± 3.35	0.00	57.05
	% Killed (2017–2019)	Percent of total growing stock killed by bark beetles (%)	5.44 ± 6.58	0.26	57.05
	Slope	Slope of trend line in % Killed over the period 2017–2019	2.51 ± 2.81	−2.27	12.88
Predictor variables	Spruce%	Spruce proportion (%)	49.17 ± 23.59	0.15	85.98
	Age	Mean spruce age (yrs)	76.45 ± 9.94	36	98
	T	Mean annual air temperature (1980–2010) (°C)	8.01 ± 0.79	6.22	9.66
	P	Mean annual precipitation sum (1980–2010) (mm)	679.59 ± 123.82	486.93	1 100.69
	Wind	Growing stock affected by wind and salvaged (m^3)	37,515 ± 74,273	27	1 091 830
	Wind_{-1}	Growing stock affected by wind and salvaged, one-year lag (m^3)	36,804 ± 75,598	0.31	1 091 830
	Tanom	Temperature anomaly; difference between T in actual year and average T over period 1980–2010	0.69 ± 0.68	−1.08	2.13
	Panom	Precipitation anomaly; difference between P in actual year and average P over period 1980–2010	96.96 ± 15.73	58.3	154.01
	Tanom_{-1}	Tanom, one-year lag (°C)	0.64 ± 0.67	−1.08	2.13
	Panom_{-1}	Panom, one-year lag (%)	97.25 ± 16.02	58.3	154.01
	SPEI	Standardized Precipitation-Evapotranspiration Index (evapotranspiration by Thornthwaite, 1948)	−0.46 ± 1.17	−5.29	2.17

Appendix B. Inter-annual variation of selected climate variables

See Fig. B1

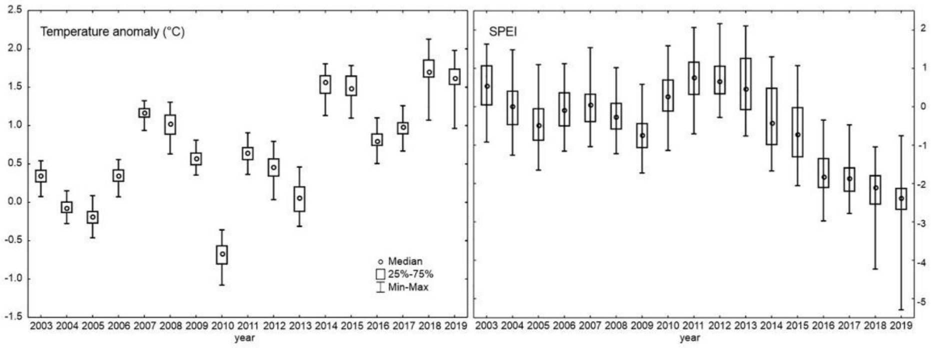

Fig. B1. Annual values of temperature anomaly (deviation from the average over the period 1980–2010) and the Standardized Precipitation-Evapotranspiration index. The range of values reflects the differences between the LAU1 districts in the Czech Republic (n = 77).

Appendix C. Frequency of occurrence of the Czech word “bark beetle“ on the Internet

See Fig. C1

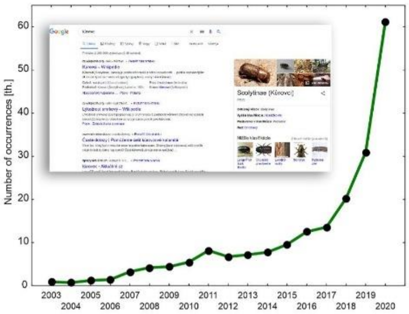

Fig. c1. The frequency of occurrence of the Czech terms for bark beetle “kůrovec“ and “lýkožrout“ over the period 2003–2020.

Appendix D. Selected economic indicators of the forestry sector in the Czech Republic

See Figs. D1, D2 and D3

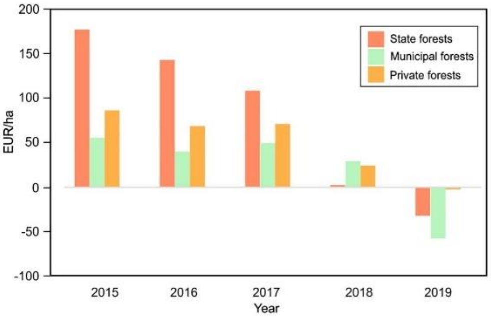

Fig. D1. Economic balance of main categories of forest owners during the recent outbreak period. The annual balance per forest area is indicated. The presented values do not include any subsidy payments (Ministry of Agriculture of the Czech Republic, 2020, 2019, 2018, 2017, 2016).

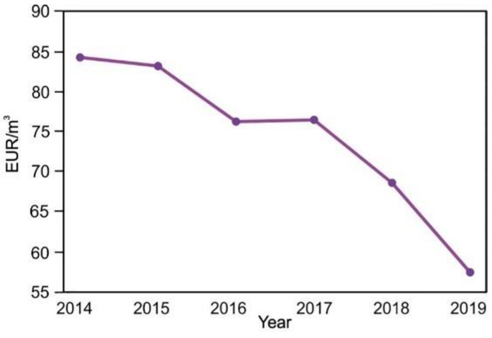

Fig. D2. Average price of spruce logs during the recent outbreak period (Ministry of Agriculture of the Czech Republic, 2020, 2019, 2018, 2017, 2016).

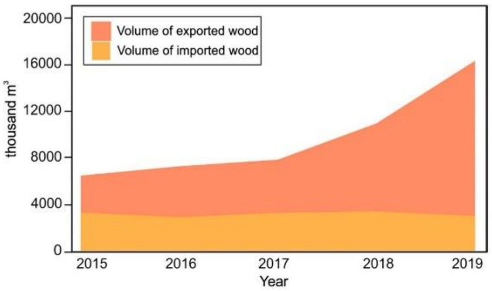

Fig. D3. Annual volume of exported and imported raw wood in the Czech Republic during the recent outbreak period (Ministry of Agriculture of the Czech Republic, 2020, 2019, 2018, 2017, 2016).

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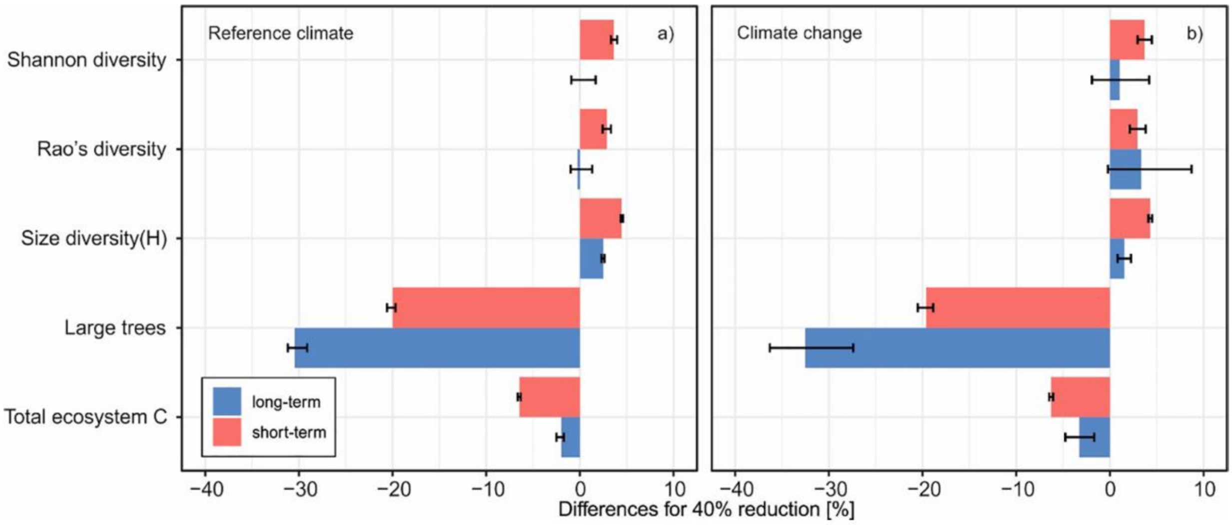
6 Diskuze

Předkládaná práce je souborem publikovaných vědeckých studií, kdy každá obsahuje relativně obsáhlou diskuzi problematiky. Diskutovány tak budou klíčové oblasti jednotlivých studií a jejich problematiky.

6.1 Zkracování doby obmýtí jako nástroj managementu kůrovcových disturbancí

Výsledky ukazují, že zkrácení doby obmýtí snižuje podíl zralých stromů, a tím je zároveň sníženo i riziko jak větrných, tak kůrovcových disturbancí. Tento nástroj však není schopen zcela zabránit vyššímu výskytu kůrovcových gradací, které jsou zapříčiněny probíhající změnou klimatu. Pozitivní vliv zkrácení doby obmýtí na přítomnost stromů náchylných k poškození větrem se projeví na množství materiálu vhodného ke kolonizaci kůrovci. Tento poznatek byl jen potvrzením již dříve udávaných výzkumů (Jactel et al., 2009; Moore and Quine, 2000). Výzkum *Ips typographus* ukázal preferenci tohoto kůrovce pro starší stromy s větším průměrem (Hlásny and Turčáni, 2013; Netherer et al., 2019; Netherer and Nopp-Mayr, 2005). Překvapivým zjištěním této studie je, že snížení doby obmýtí snižuje riziko působení větrné disturbance efektivněji než kůrovcové (-18 % větrná disturbance, -11 % kůrovcová disturbance). I při zkrácení doby obmýtí o 40 % zůstává v krajině stále kritický počet hostitelských stromů, přičemž při změně klimatu je tento rozdíl ještě výrazně větší (-25 % oproti -0,7 %). Tento výsledek zdůrazňuje, že i nižší množství vhodných hostitelských stromů je při silné gradaci kůrovce stále rizikovým faktorem a jejich přítomnost v krajině nelze podceňovat (Honkaniemi et al., 2020). Tato analýza však nezohledňuje škodlivé činitele zaměřující se na mladší stromy, jejichž četnost se se zkracováním doby obmýtí bude zvyšovat. Mladší stromy budou více ovlivněny jak biotickými (např. *Hylobius abietis* (Leather et al., 1999)), tak abiotickými faktory (např. sucho (Kolb et al., 2016)).

Doba obmýtí má vliv na mnoho částí lesního ekosystému, například půdu, ukazatele biodiversity, uhlík a v neposlední řadě produkci dřeva (Felton et al., 2017; Kaipainen et al., 2004; Roberge et al., 2016). Současné působení změny klimatu musí být bráno jako součást lesnického plánování (Luyssaert et al., 2018) a management by tak měl být volen s ohledem na vedlejší efekty jako je zásoba uhlíku (Pilli et al., 2016). Uhlík je sníženým obmýtím ovlivněn především krátkodobě, přičemž stejné výsledky uvádí i předchozí studie (Kaipainen et al., 2004; Liski et al., 2011). V provedených simulacích účinek vázání oxidu uhličitého stromy, a tím navýšení ukládání uhlíku v lese v rámci změny klimatu, dokázal kompenzovat ztrátu uhlíku zkráceným obmýtím (Obr. 3). Tento jev, tolik důležitý v bilanci uhlíku, je nutné zvážit v přístupu managementu lesa (Bellassen and Luyssaert, 2014). S ohledem na ukazatele biodiverzity se kratší obmýtí projevuje jako nástroj s možným negativním dopadem. Odstraňování starších stromů je zásadním faktorem pro množství druhů, které se mimo tyto podmínky nevyskytují (Felton et al., 2017; Hilmers et al., 2018).



Obr. 3 Vedlejší efekty způsobené snížením doby obmýtí o 40 %. Zobrazen je efekt krátkodobý (průměr prvních 30 let simulace) i dlouhodobé dopady (průměr hodnot zbývajících 170 let). Sloupce zobrazují střední hodnoty opakovaných simulací a rozdílných klimatických scénářů. Úsečky označují 10–90% kvantil.

Studie ukázala že 40% zkrácení obmýtí sníží o 30 % zastoupení stromů s průměrem nad 60 cm ve výčetní výšce. (Obr. 3). Bude-li tento managementový zásah využit, je možné jako náhradu tohoto negativního dopadu na biodiverzitu zvyšovat podíl chráněných území (Felton et al., 2017). Změna jednodruhových stanovišť k diversifikovanému porostu však může poskytnout možnosti novým druhům s jinými potřebami habitatu a vést lesní ekosystémy k adaptaci na změnu klimatu (Bouriaud et al., 2015; Thom et al., 2017b).

6.2 Nahodilá těžba jako nástroj managementu lesa a možnosti jejího plošného rozmístění

Simulace ukázaly, že k efektivní redukci šíření kůrovce může vést pouze její provádění v nejvyšší možné intenzitě. V oblastech, kde je třeba zachování vysoké úrovně smrku je intenzivní nahodilá těžba vhodným opatřením. Toto zjištění se shoduje s předchozími výzkumy nahodilé těžby ve střední Evropě, jejichž cílem je snížit množství vhodného hostitelského materiálu k šíření kůrovce (Hlásny and Turčáni, 2013; Økland et al., 2016). Efektivita provádění tohoto nástroje managementu prudce klesá s hodnotou intenzity provádění menší než 95 %. Ponechání i malého množství stromů poškozených větrem tak může vést k podmínkám vhodným k epidemickému šíření (Kausrud et al., 2012; Marini et al., 2017).

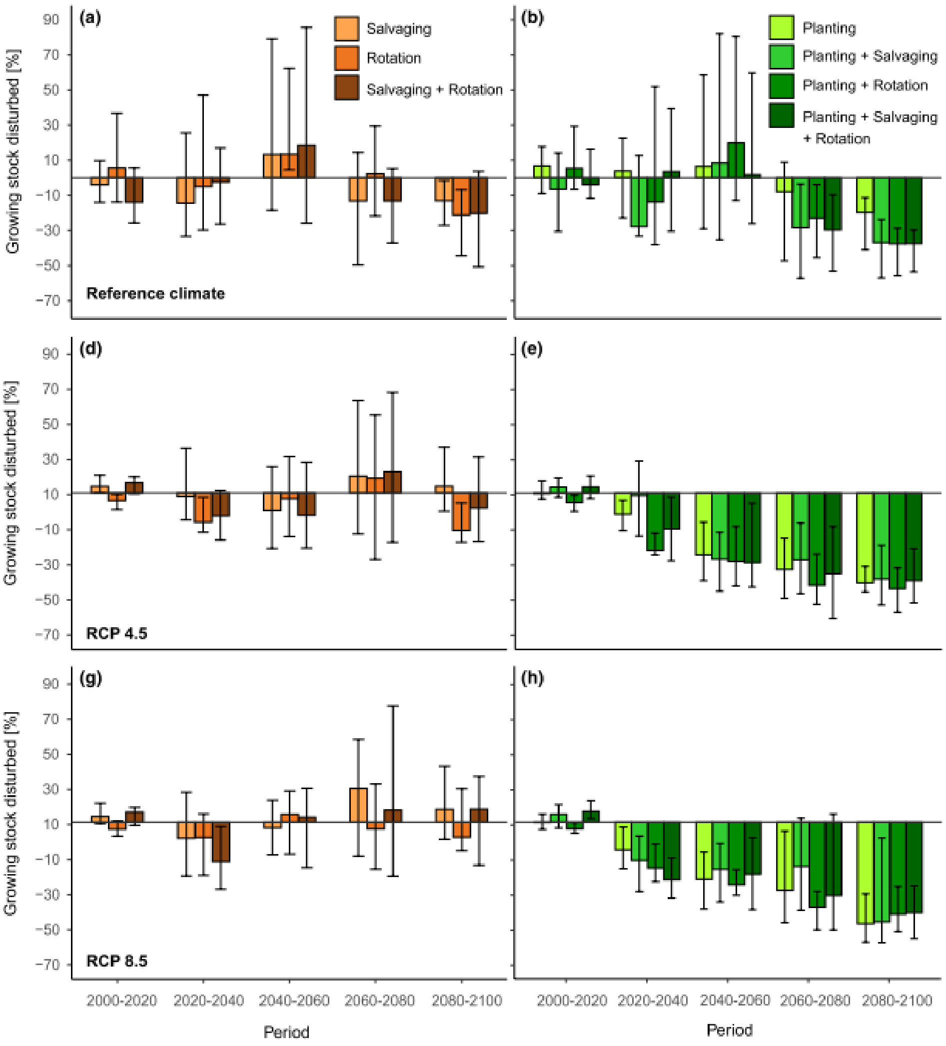
V rámci výzkumu byl zjišťován i vliv prostorového rozmístění nahodilé těžby. Některé státy jsou limitovány v těžbě infrastrukturou lesních cest. Při umístění těžby v okolí 120 a 200 metrů kolem dobře přístupných částí lesní cestní sítě se tento způsob ukázal jako neefektivní a šíření kůrovce nesnížil. Vzhledem k tomu, že efektivní disperzní oblast kůrovce je 500 m (Kautz et al., 2011; Potterf et al., 2019), by bylo třeba oblast provádění managementu kolem cest rozšířit, aby se tento přístup mohl případně projevit jako efektivní. Design, kdy byl management prováděn ve vybraných blocích by měl napomoci k lepšímu pochopení problematiky možného šíření kůrovce z bezzásahových zón do sousedních obhospodařovaných porostů (Potterf et al., 2019; Potterf and Bone, 2017). Simulace prokázaly, že vliv kůrovců na plochy s managementem ve vybraných blocích byl snížen stejně v porovnání s aplikací tohoto managementu plošně. Pokud bude salvage logging prováděn na vybraných částech porostu ve vysoké intenzitě, tyto porosty by neměly být zvlášť ovlivněny ponecháním mrtvého dřeva v bezzásahových zónách. Klimatická změna ovšem veškeré efekty prostorového rozmístění těžby markantně snížila.

Simulace navíc prokázaly, že nahodilá těžba prováděná ve vysoké intenzitě může na jednu stranu snížit dopady kůrovcové gradace, na stranu druhou ovšem jsou porosty více náchylné k poškození větrem. To je způsobeno přítomností vyspělých smrků a rozvolněním porostu, přičemž tyto faktory jsou s ohledem na větrné disturbance rizikové (Jactel et al., 2009; Wermelinger, 2004). Salvage logging by měl být prováděn pouze za specifických podmínek. Je vhodnou volbou za předpokladu, že je možná jeho implementace ve vysoké intenzitě, přičemž je třeba počítat s vyšší finanční náročností, pokud budou větrem poškozené plochy velké a rozptýlené (Seidl et al., 2019). Předpoklady k jeho využití však se změnou klimatu budou nastávat méně často a šíření kůrovce bude probíhat i bez stromů poškozených větrem. Jedním z hlavních důvodů může být nedostatek vody a častější a delší období sucha (Netherer et al., 2015; Sommerfeld et al., 2018).

Celkový uhlík v krajině se s vyšší intenzitou salvage logging sníží jen velmi mírně, vzhledem k porovnání množství uhlíku odstraněného těžbou a na druhé straně uhlíkem, který díky předejití dalším škodám v budoucnosti zůstal zachován v porostu. Díky snížení poškození dochází k zachování většího množství živého uhlíku v nepoškozených stromech. Podobné účinky byly pozorovány také Bradfordem et al. (2012). V simulacích byl podstatněji znát vliv změny klimatu na celkovou zásobu uhlíku, než vliv provádění nahodilé těžby. Za podmínek změny klimatu bude tak důležitým faktorem spíše vedení porostů do podoby s větší resiliencí a opatření managementu jakožto krátkodobější řešení budou ustupovat do pozadí.

6.3 Hodnocení kombinací nástrojů managementu v podobě nahodilé těžby, zkrácené doby obmýtí a postupné změny dřevinné skladby

V porostech s dominancí smrku v podmínkách změny klimatu se může intenzita disturbance zvýšit o 140–170 % a podíl smrku v takto poškozeném porostu rychle klesá. Tento výsledek simulací nastiňuje možné důvody současného rozpadání smrkových lesů v Evropě, kde se střední Evropa stala epicentrem v důsledku změny klimatu a velkých disturbancí (Hlásny et al., 2021, 2019; Senf and Seidl, 2018). V předešlých letech nebylo klima tak negativním faktorem. Disturbance nebyly tak intenzivní a bylo možné je zpomalit nebo zastavit za pomoci aktivního managementu. Během zintenzivňování disturbancí, které klima přináší, však tyto metody nebudou dostačující za předpokladu, že nebudou prováděny ve velmi vysokých intenzitách (v simulacích alespoň 90% intenzita odstraňování větrem poškozených stromů a 40% zkrácení doby obmýtí). Výsledky studie prokázaly, že při managementu lesa vedoucímu k diversifikovaným porostům nebude působení disturbancí na tak kritických hodnotách jako tomu je u stejnorodých porostů, a to dokonce úplně bez zásahů aktivního managementu jako je právě salvage logging a zkracování doby obmýtí. Shodně s dřívějšími studiemi bylo zjištěno, že změna v druhovém složení porostů od monospecifických k diversifikovaným bude v managementu za podmínek změny klimatu stěžejním faktorem (Jandl et al., 2019). V porovnání s monospecifickými ekosystémy vykazují diversifikované porosty nižší zasažení disturbančními činiteli (Griess et al., 2012; Neuner et al., 2015) a jsou také vhodnější k poskytování ekosystémových služeb (Mori, 2017). Je třeba volit správnou kombinaci postupů aktivního a pasivního managementu k nalezení největší efektivity v porostu (Obr. 4). Zdá se, že by bylo možné vyhnout se opatřením aktivního managementu jako je zkracování doby obmýtí a salvage logging, což by mohlo mít pozitivní dopad na lesnickou ekonomiku i dynamiku ekosystémů.



Obr. 4 Relativní rozdíly mezi porostem zasaženým větrnou nebo kůrovcovou disturbancí s využitím různých kombinací jejich managementu a simulací se základním managementem bez opatření zmírňujících dopady disturbancí. Grafy v levém sloupci (hnědé) ukazují vývoj v porostech, kde je využíváno hospodaření s převahou smrku. Grafy v pravém sloupci (zelená) ukazují vývoj v porostech se změnou dřevinné skladby blíže přirozené skladbě.

Zachování dlouhého obmýtí nebo jeho prodloužení může mít pozitivní vliv na ukazatele biodiverzity a koloběh uhlíku (Roberge et al., 2016; Thom et al., 2019). Omezení salvage logging a zachování mrtvého dřeva v lese podporuje funkce regulace podnebí a vody, zvyšuje biodiverzitu i u druhů kůrovcových antagonistů a zachovává zásoby uhlíku uloženého v mrtvém dřevě (Lassauce et al., 2011). Jako východisko zvýšení stability lesního ekosystému se tak nabízí adaptivní obhospodařování lesů zvýšením druhové a strukturální rozmanitosti. Avšak nahrazení vysoce produktivních, zároveň ale zranitelných druhů stromů druhy tolerantnějšími ke změnám klimatu a méně rizikovými, může znamenat nežádoucí negativní dopad na ekonomickou sféru lesnického sektoru (Brang et al., 2014). V možnosti pokračovat částečně v hospodaření smrku může být řešením genetická variabilita smrku. K jeho pěstování za změny klimatu by mohlo přispět využívání provenience smrku tolerantní vůči suchým a teplým podmínkám (Jandl et al., 2019).

6.4 Vývoj kalamity kůrovce v České republice a její dopady na ekologickou, ekonomickou a sociální sféru a využití patogenů v boji s kůrovcem

Většina disturbancí v Evropě byla ve velké míře spuštěna předcházejícími projevy větru (Lausch et al., 2013; Mezei et al., 2017; Modlinger and Novotný, 2015), jejich šíření však bylo také pravděpodobně synchronizováno kolísáním klimatu a dalšími faktory (Økland et al., 2005; Senf and Seidl, 2018). Studie problematiky gradace potvrdila, že nedávné markantní zhoršení situace kůrovcových disturbancí nebylo přímo propojeno s větrnou kalamitou, protože účinek větru byl významný v celém období 2003–2019, avšak ohniska z období 2015–2020 nebyla přímo navázána na větrné události. Prominentní roli v rozvoji gradace zde zřejmě hrál vliv sucha. Marini et al. (2017) také uvádí že sucho v kombinaci s oteplováním může napomoci růstu populací kůrovců i bez spojení s větrem. Studie také prokázala v České republice velký nárůst gradace ve velmi suchém roce 2015 a stejný průběh měl také klimaticky extrémní rok 2018. S tím souvisí zjištění, že v roce 2018 byla v Evropě pozorována za posledních 34 let největší mortalita porostů, přičemž kůrovcové disturbance jsou jedním z důvodů (Senf et al., 2020). Budoucí vývoj gradace je vzhledem k nepředvídatelnosti klimatických extrémů nejasný. Nemůže být očekáván její kolaps vzhledem k stále velkým plochám smrkových porostů. Spíše se předpokládá zvětšování epicentra gradace nebo jeho přesun do míst s dostatkem zdrojů při jejich vyčerpání v současné lokalitě. Pohonem pro další zhoršení situace bude pravděpodobně na základě projekcí předpokládané zhoršení klimatických extrémů, včetně dlouhých a častějších období sucha (Grillakis, 2019).

Epidemická situace kůrovce působí ve většině případů negativně na vztahy mezi managementem a s ním svázanými sektory jako je ochrana přírody, myslivost, trh práce nebo problematika dopravy. Tento stav je způsoben pravděpodobně díky nesouladu přístupů lesnického managementu a plánování a ačkoli politické úsilí o vyřešení těchto problémů je v současnosti intenzivnější, v rychlém šíření gradace je i tato snaha zatím nedostačující (Hoogstra-Klein et al., 2017; Maier and Winkel, 2017). Gradace však na druhé straně také zvýšila zájem o povědomí problematiky, zapojení veřejnosti a také podnítila postupnou transformaci legislativy.

Výzkum patogenu *Larsoniella duplicati,* který je specifický pro invazního kůrovce *Ips duplicatus* sleduje gradient zeměpisné výšky a šířky. I když mikrosporidie zkoumaná ve studii nemá značný negativní dopad, její virulence může mít určitý dopad na jeho invazní úspěchy. V biologickém boji a v omezení šíření kůrovců nemohou v současném stavu hrát přirození nepřátelé velkou roli díky jejich omezenému dopadu a složité aplikaci v terénu a mohou pouze urychlit kolaps gradací u populací, které již ustupují (Holuša and Lukášová, 2017).

7 Závěr a doporučení pro praxi

Tato disertační práce hodnotí účinnost vybraných nástrojů managementu lesa, jejich pozitivní, ale i negativní dopady. Současně také poukazuje na nové poznatky z oblasti populační dynamiky kůrovců a shrnuje a mapuje vývoj kůrovcové kalamity v České republice.

Změna klimatu značně snižuje účinnost všech opatření managementu a je třeba tak zvážit jejich vhodnost pro konkrétní situace a případnou kombinaci několika opatření. Při hledání vhodných opatření a nástrojů managementu větrných a kůrovcových disturbancí je třeba pečlivě zvažovat jejich přínos, efektivitu, avšak i negativní vliv na lesní ekosystémy.

Zkrácení doby obmýtí může být v podmínkách lesů střední Evropy v kontextu změny klimatu vhodným nástrojem managementu. Praktické uplatnění tohoto opatření však vyžaduje mnohem širší perspektivu (Bolte et al., 2009; Jactel et al., 2009). Kratší obmýtí je možné uplatnit zejména v rizikových oblastech. A samotné zkracování obmýtí by mělo být důležitou součástí celkové přestavby porostů (Sousa-Silva et al., 2018). Salvage logging je v mnoha částech střední Evropy již používán. Tento nástroj je vhodný k omezení šíření kůrovcových disturbancí a zachování uhlíku v živých stromech, ale jeho efektivita souvisí s tím, že musí být prováděn v intenzitách zásahu 95 % a více. Tedy lze jej provádět především u disturbancí malého rozsahu, které jsou prostorově koncentrované.

Zranitelnost monospecifických a diversifikovaných porostů vůči disturbancím se značně liší, přičemž změna klimatu tyto rozdíly ještě prohlubuje. Zdá se, že za změny klimatu vedoucí k častějším projevům klimatických extrémů bude vhodné v budoucnosti využívat spíše pasivních dlouhodobějších nástrojů managementu, které budou posilovat odolnost porostů vůči všem disturbančním činitelům a povedou k celkové resilienci lesa. Jako vhodné řešení se zde tedy projevuje pěstování druhově, věkově i prostorově diversifikovaných porostů, které budou méně náchylné k poškození disturbancemi. Lesní ekosystémy vznikající z takovýchto porostů mohou být výhodné i z hlediska ukazatelů biodiverzity, koloběhu uhlíku a budou splňovat potřeby sociálních služeb. Vzhledem k dlouhodobému časovému horizontu, v jakém lesní ekosystémy fungují, může být účinek takového managementu opožděn, a proto je možné souběžně využívat i další nástroje jako odstraňování hostitelského materiálu z porostu, dřívější těžba rizikových porostů nebo odchyt brouků.

Ve vzorci vývoje kůrovcové gradace v České republice se zřetelně projevil posun od ohnisek způsobených větrnými kalamitami ke škodám způsobeným díky vlivu sucha, ovlivněného klimatickou změnou. Menší, spíše lokální kůrovcová ohniska se také změnila v problematiku dynamiky ohnisek regionálních až mezinárodních. Je třeba zdůraznit nízkou šanci v ohledu udržitelnosti produkčního pěstování porostů složených převážně ze smrku ztepilého, přičemž se jedná o způsob pěstování široce rozšířený ve střední Evropě. Nynější gradační situaci tak můžeme spíše pokládat za počátek přeměny smrkových monokulturních porostů v jiné diferenciované porosty, které budou lépe připraveny čelit měnícímu se klimatu, a i v kritických podmínkách prostředí se bude jednat o lesy s větší odolností.

V současné situaci a za předpokladu klimatické změny s přibývajícími klimatickými extrémy, fakta v této práci naznačují, že dosavadní východiska managementu lesních porostů je třeba přehodnotit a posunout se směrem k plánování porostů v rámci širšího hlediska krajiny a nové porosty směřovat dlouhodobě k odolnosti vnějším nepříznivým podmínkám. Implementací nových postupů se tak bude tradiční lesnictví tak jak ho známe postupně měnit.

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