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NATURAL CONDITIONS FOR HELIOPHILOUS TREE-SPECIES FOLLOWING FOREST DIEBACK IN TEMPERATE ZONE AFTER PERIGLACIAL HABITATS

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ABSTRACT

Widespread forest dieback following a series of exceptionally dry seasons has made restoration by relic heliophilous tree-species uncertain. Using logistic regression, we identified conditions suitable for relic Norway spruce (*Picea abies* /L./ Karst.), Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.), birches (*Betula* sp.), poplars (*Populus* sp.) and willows (*Salix* sp.) by comparing the relief and bedrock under stands that died abruptly between 2018 and 2020 at temperate zone after periglacial habitats of the Czech Republic. Extent of forest dieback was determined through automated object analysis on the basis of vectorised Planet Scope and Sentinel-2 satellite images. The object analysis consisted of mainly spruce stands and dieback indicated by a deep inter-year decrease in the vegetation indices. The overall occurrence of tree-species in pure or mixed stands was determined from a polygon geodatabase of forest management plans, while growth condition types were determined by overlaying biogeographically subdivided polygons. Dead forests provided suitable conditions for mixed conifer, birch, and poplar stands on 64.4 % of the greywackes, acid metamorphites, and waterlogged sediments on broken plateaus, depressions, and slopes. In comparison, pure stands of relic tree-species can cover 35.6 % of dead forest area. Restoration of mixed forests differenting over a range of growth conditions seems to be suitable for adaptation to climate change impacts.

Keywords: acidic bedrock; relic glacial species; *Ipinae*; temperate forests; forest restoration

INTRODUCTION

Today, the natural forest tree composition in temperate climatic zone consists of a species mixtures that survived the ice ages (glacials) or spread during the interglacial Holocene period (Puhe & Ulrich, 2001). While glacial plant species are heliophilous and occur mainly in tundra, the interglacial species are often heliophobic to form dense forests. Subsequent

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forest conversion has tended to be suppress original tree-species competitions (Pretzsch *et al*., 2014). Because economically converted forests are more susceptible to effects of climate change, decaying stands offer space for the spread of heliophilous tree-species (Paoletti *et al*., 2010). In addition to opening up such sites, global warming also threatens cold-tolerant glacial species (Augustin *et al*., 2005; Puettmann & Ammer, 2007; Vacek *et al*., 2017). For these reasons, the site characterisation for individual tree-species becomes a necessary tool estimating potential forest vulnerability to recent climate change (Taberlet *et al*., 1998).

Modern forest tree-species communities have naturally shifted by geotectonic movements and climate changes. The cyclical alternation of glacial and interglacial periods caused dominant tundra or steppe to replace by forests, whereas neotectonics meant that plant communities never changed at the same range (Krzyszkowski *et al*., 2000). European glacials were followed by unprecedent north-south transient shortening from periglacial deserts to tundra, forest-tundra, steppe and forests (Puhe & Ulrich, 2001). By the last glacial, the present-day biogeographical provinces had become established (Tarasov *et al*., 2000).

Present-day temparate vegetation is mainly result of natural adaptation to three periods since last glacial maximum (LGM), late glacial to Holocene. During the LGM, temperate Europe was covered by larch (*Larix* sp.) tundra with birch (*Betula* sp.) quickly making use of temporal interstadial warming to form birch-larch forest-tundra. This forest-tundra was then enriched with more demanding trees from genera including hazel (*Corylus* sp.), elm (*Ulmus* sp.), oak (*Quercus* sp.) or hornbeam (*Carpinus* sp.) in suitable valleys (Müller *et al*., 2003). The maximum interstadial warming encouraged the establishment of conifers such as spruce (*Picea* sp.) and pine (*Pinus* sp.) and alder (*Alnus* sp.) to creating a predominantly coniferous taiga. Cooling during transition between LGM and late glacial was followed by surviving pine with oaks and hornbeams (Binney *et al*., 2017). The most important Central-European transient zone was mainly covered by steppe with residual pine-birch stands, while Carpathian or perialpine valleys were forested with pine-larch taiga and spruce forests (Pokorný *et al*., 2015). In intermountain valleys, the termophilic species such as hazel, alder, elm, oak, Common beech (*Fagus sylvatica* L.), European hornbeam (*C. betulus* L.), Silver fir (*Abies alba* Mill.), linden (*Tilia* sp.) and maple (*Acer* sp.) have kept (Jankovská & Pokorný, 2008).

The Holocene is unique by permeation of vegetation natural development with human transformations of the landscape. The vegetation development after deglaciation started by rapid contact between cold-tolerant and termophilous species. Return of termophilous tree-species began by hazel, oaks and elms, which transformed indigenous forest-tundra to predominantly oak-pine forests (Neuhäuslová *et al*., 1998). Holocene optimum culminated by spreading of mixed oak-woods in lower altitudes and by mixed lime-maple-beech forests in higher altitudes (Prentice *et al*., 1996). The broadleaved dominance was interrupted due to spreading of spruce during cooling in Middle Holocene. Consequential climate drying in Upper Holocene was followed by beech and fir spreading both into hornbeam-oakwoods in lower altitudes and into spruce forests in mountain altitudes (Magri *et al*., 2006).

Manmade transformations of the landscape began with deforestation around early settlements and hunting grounds, but they were not followed by tree outplanting until the end of the Middle Age. Forest fragmentation converted former glacial forestless areas into a mosaic of transient habitats, along them biodiversity increased (Pokorný, 2005). The later Medieval forests were reduced to the borderlands in remote mountain systems or were maintained as hunting greenwoods. Heliophobic species have yielded to more resistant oaks, hawthorns (*Ostrya* sp.), hazel, birches, alders, willows (*Salix* sp.), Common beech and Norway spruce (*P. abies* /L./ Karst.) (San-Miguel-Ayanz *et al*., 2016). Subsequent raking of

litter, afforestation with homogeneous pine or spruce stands and establishment of large fields decreased landscape biodiversity (Whitehouse, 2006).

Our study focused on estimate of glacial tree-species site availability in Central-European conditions following forest dieback. Cleared sites are immediately colonised by heliophilous species, that similarly covered glacial steppes at the beginning of the interglacial periods. The forests planted out of natural conditions die during climatic change after dry episodical events. Consequent dieback is caused by pathogens preferentially attacking drying trees (Paoletti *et al*., 2010). Forest dieback due to unadaptability to climate change conditions uncertain survival for relic glacial tree-species on cleared areas (Lindner *et al*., 2010). The similarities between relic and cleared sites suggest probability of glacial refugia expansion, while differences suggest unsuitable areas (Feest, 2006). Assessment of growth conditions for cold-tolerant tree-species after forest dieback was limited to species occuring at former periglacial zone continuously since the Holocene beginning. The selection of the periglacial conditions was adapted to include corridor under cyclic biome alternations during Quaternary environmental changes (Pokorný *et al*., 2015).

MATERIAL AND METHODS

Processing framework

Sites for glacial tree-species under conditions of forest dieback was indicated through regression models in the Czech Republic (CR) (78,866 km^2; 115–1602 m n.m.; 48.569–51.021N; 12.102–18.863E). This Central-European country is situated in temperate climatic zone of the northern hemisphere comprising major part of Hercynian biogeographic subprovince (84.7 % of the total area) with lesser parts within the Polonian (2.2 %), Carpathian (9.0 %) and North-Panonnian (4.1 %) subprovinces. At the present time, forest covers over 37 % of the country's area (Máslo *et al*., 2023). Margins between Hercynian and Carpathian subprovince represent unique migration corridor for biota travelling between Baltic and Mediterranean seas. This corridor connected Hercynian and Carpathian refuges of termophilous interglacial biota otherwise hidden in the deep valleys of these highlands (Pokorný *et al*., 2015).

The site distribution was assessed for coniferous Norway spruce (*Picea abies* /L./ Karst.), Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.) and broadleaved birch (*Betula* sp.), willows (*Salix* sp.) and poplars (*Populus* sp.), which formed early succession forest stages in Central-European highlands since the late glacial thanks to absent disturbances after large herbivor migrations or after burnings (Jankovská, 2006). During the Holocene, the natural proportion of Norway spruce reached around 10.9 %, Scots pine 3 %, European larch less than 0.01 %, birch 1.3 %, willows 0.3 % and poplars 0.1 % (Šindelář, 1995). In contrast, total proportion of modern-day converted forests of Norway spruce is 48.8 %, Scots pine 16.1 %, European larch 3.9 %, birch 2.8 %, willows less than 0.1 % and poplars 0.3 %. All of these tree-species are able to occupy cleared soil, where they have low nutrition demands with only spruce being more demanding as regards water availability (San-Miguel-Ayanz *et al*., 2016).

The fastest decline of Norway spruce from total proportion exceeding 50 % happened after extraordinary dry seasons 2015 and 2018 with overpopulated bark-beetles (*Ipinae*) in the CR (Hlásný *et al*., 2021). Effects of overpopulated bark-beetles culminated in 2020, when 14,620 km^2 (54.4 %) of forests were totally damaged. The volume of sanitary fellings reached more than 46 million m^3 of timber during disaster period 2015–2020 with 15 million m^3 felled in

2020 alone. At the same time, the proportion of timber attacked by bark-beetles increased from 29.9 % of sanitary fellings to 76.6 % in 2020 (Knížek & Liška, 2021).

Data

Comparison of growth conditions was carried out among vector overlays of culminating bark-beetle damage and tree-species coverage with relief and bedrock types. The culmination of forest dieback ceased around 2018–2020, when the dry episode was interrupted by an extremely wet season (Trnka *et al*., 2022). Forest dieback range was assessed through object analysis of Planet Scope satellite images at resolution 3×3 m over spruce occurences and of Sentinel-2 data suggesting forest collapse (Hájek *et al*., 2019). Current spruce occurence > 50 % was restricted to stands > 12 m tall on the basis of differences between normalised forest cover and digital elevation model at resolution 2×2 m (Lukeš *et al.*, 2018). Forest dieback was assessed through decrease in leaf area index over 1.5 between two subsequent observation years. Abandoned dead forests and clear-cuttings before mandatory afforestation were distinguished through triangular greenness index values (Lukeš, 2021). Raster images of abandoned and felled stands were vectorised automatically along abrupt changes in vegetation indices.

Tree stands for investigation were selected from a database of forest management plans established by the Forest Management Institute Brandýs nad Labem. Tree-species proportion was categorised as pure > 90 %, dominant 50–90 % or mixed < 50 % (Pommerening & Grabarnik, 2019). The influences due to forest conversion to wood occurrence out of suitable sites were verified by subtraction from reserves using Unified Environmental Information System (San-Miguel-Ayanz *et al*., 2016). Pure spruce stands represented 44.3 % of total spruce occurrence and pine stands 29.4 % of total occurrence, while pure larch stands just 3.6 % and pure broadleaved stands represented 0.1–0.2 % (Fig. 1). Conserved spruce populations represented just 4.5 % of total occurrence and conserved pine or larch stands both represented 2.8 %. Stand sites were obtained from typified relief and bedrock polygon overlays.

Typified relief and bedrock polygons were taken from biogeograpical register established by the Nature Conservation Agency of the Czech Republic (Culek & Grulich, 2009). The area of the CR is covered by 18 relief types along with 23 non-waterlogged and eight waterlogged bedrock types. The forest cover supermajority was divided along broken plateaus (26.3 %), slopes (17.7 %) and highlands (12.8 %) with the most common bedrock types of acid metamorphites (26.1 %), greywackers (11.2 %), acid plutonites (7.9 %), acid waterlogged sediments (7.1 %), neutral plutonites (7.3 %) and various metamorphites (7.2 %).

Statistical modelling

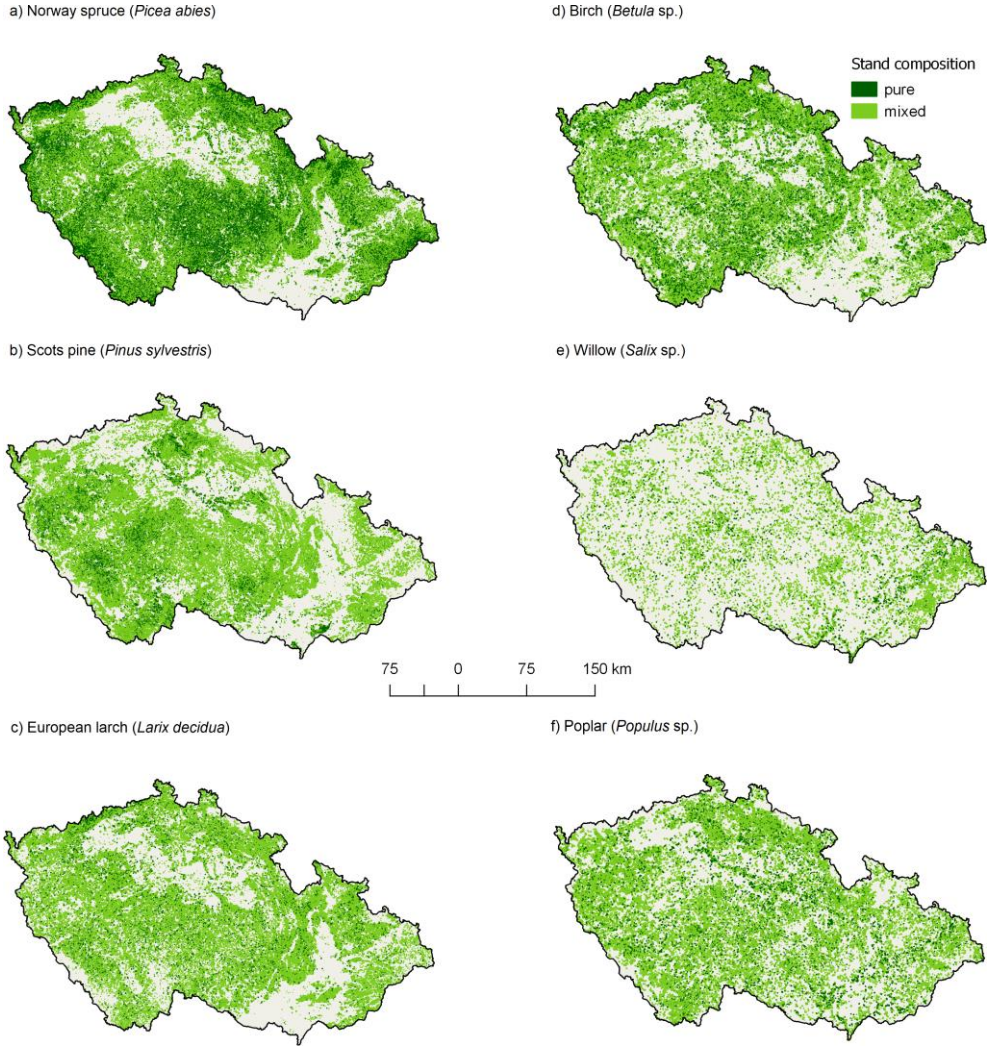
Statistical modelling on site availability for relic glacial tree-species following forest dieback was carried out through simultaneous linear and logistic regressions at $p < 0.05$. Linear regression was used to assess similarity between growth conditions closed intervals in tree stands and dead forests. In contrast, logistic regression was used to assess the probability of glacial species spreading to damaged forests (Svenning *et al*., 2008):

$$CSS = \frac{e^{a.TSO+b}}{1+e^{a.TSO+b}},$$

where the *CSS* represented cleared site suitability, the *TSO* was tree-species occurence, *a* was direction and *b* was asymptote. The proportion of independent tree variables was specified as absolute values, while site dependent variable were simplified from 0 for the

least presented type to 1 for the most presented type. Significant models were indicated by a determination index (R^2) > 0.5. Growth conditions were simply characterised by overlaying relief and bedrock types. The overlay composed climatic and soil conditions for forest tree-species growth to geomorphologic-bedrock bodies at various altitudes (Samec *et al.*, 2018).

Fig. 1: Relic tree-species propotion in present-day converted forests of the Czech Republic

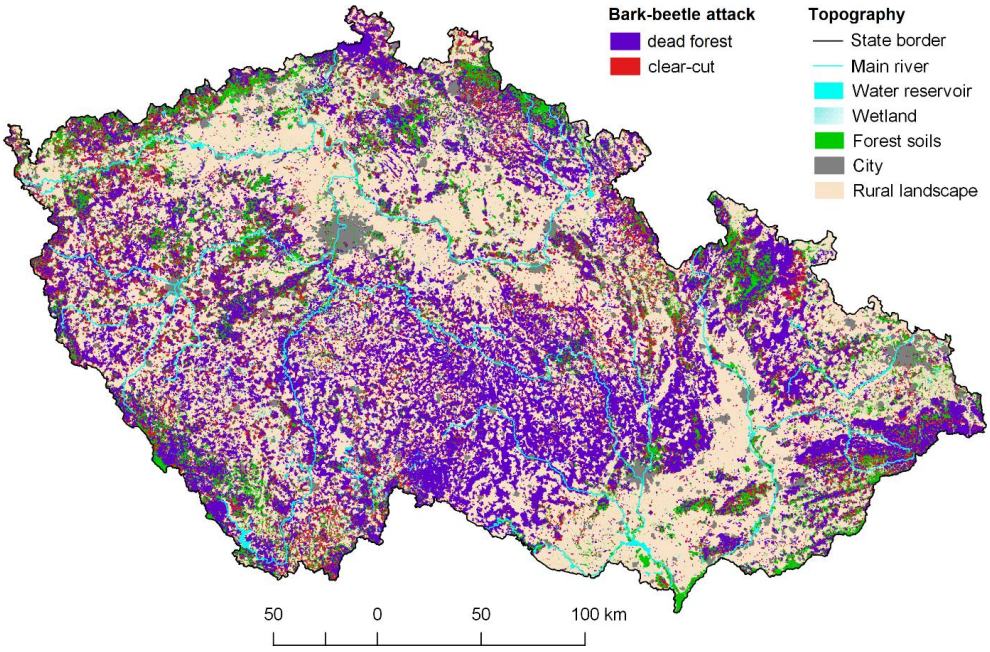


RESULTS

Comparison between growth conditions

The area of forests damaged by bark-beetles increased around 1635.5 km^2 between 2018 and 2020, when it included 11.18 % from completely died stands. Abandoned dead forests included 31.7 % from recently damaged forests, while clear-cuttings were felled at 68.3 % of attacked stands (Fig. 2). Dead forests occurred on all relief and bedrock types. The proportion of growth conditions on clear-cuttings and abandoned dead forests was similar despite markedly different ranges at both remediations. Culminating forest damage predominantly impacted broken plateaus (B), hillycountries (P) and valleys (U) at 62.1 % of the total area. The forest dieback occurred predominantly on neutral plutonites (P), acid metamorphites (S) and block sandstones (W) covering 53.8 % altogether (Fig. 3).

Fig. 2: Forest dieback due to bark-beetle overpopulation culminating during 2018 and 2020 in the Czech Republic



The proportion of growth condition types differed noticeably by tree-species. Although, the broken plateaus were dominant site for all tree-species investigated, conifers tended to be found more often in hillycountries. In contrast, willows or poplars occured similarly on plateaus, slopes, valleys and highlands (Table 1). Bedrock acid metamorphites (S), greywackes (M) and acid waterlogged sediments (AWS) were all similarly important under stands damaged by bark-beetles in contrast to relief types, which varying between tree-species sites. Nevertheless, spruce stands covered the most acid plutonites (R), greywackes, metamorphites and AWS. Willows occured the most on loamy sediments (LFS) and marl flysches (C). Poplars covered LFS, AWS and also acid metamorphites similarly (Table 2).

Fig. 3: Proportions of relief (a) and bedrock (b) types under forests of the Czech Republic in comparison to areas damaged due to bark-beetle overpopulation

Relief types: A – anthropogenic landforms; B – broken plateaus; D – depressions; H – mountains; I – separated peaks; K – cirques; L – wide floodplains; N – narrow floodplains; P – hillycountries; Q – upland rock cities; R – plateaus; S – slopes; T – waterlogged plateaus; U – valleys; V – highlands; W – highland rock cities; Y – mountain rock cities; Z – ridges. Bedrock types: A – limestones; B – marls; C – marl flysch; D – spongilites; E – loess; F – lime sandstones; H – serpentinites; I – alkaline young volcanites; J – alkaline crystallinicum; K – sandstone flysch; L – neutral perm; M – greywackes; L – loamy gravel-sands; O – neutral young volcanites; P – neutral plutonites; Q – various metamorphites; R – acid plutonites; S – acid metamorphites; T – cherts; U – gravel-sands; V- eolian sands; W – block sandstones; X – kaolinte perm.

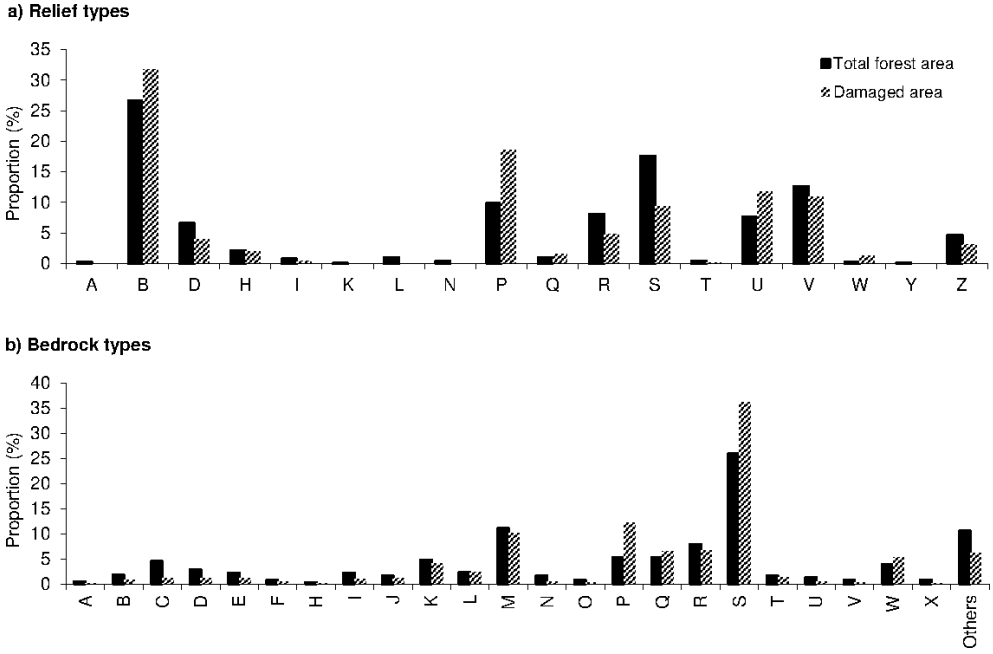


Table 1: Proportion of relief types at damaged areas and in relic tree-species stands

Relief	Clear-cuts	Dead forest	*Picea*	*Pinus*	*Larix*	*Betula*	*Salix*	*Populus*
Anthropogenic	0.14	0.04	0.01	0.08	0.50	1.10	1.16	1.29
Broken plateaus	31.74	31.71	23.68	36.93	33.52	27.30	20.28	26.17
Depressions	5.99	3.97	8.38	4.88	3.18	8.02	6.05	9.11
Mountains	2.25	2.06	2.62	0.44	2.40	1.94	1.09	1.38
Isolated peaks	0.52	0.37	0.56	0.44	1.11	1.56	0.41	1.05
Cirque	0.02	0.05	0.08	0.00	0.00	0.05	0.04	0.00
Wide floodplains	0.12	0.04	0.02	0.05	0.03	0.14	16.32	9.33
Stream floodplains	0.26	0.06	0.06	0.13	0.05	0.23	16.08	5.07
Hillycountries	13.16	18.57	10.64	10.75	11.20	8.84	7.13	8.39
Broken uplands	0.53	1.64	0.42	2.86	0.57	1.49	0.18	0.76
Plateaus	6.63	4.78	4.00	19.10	4.80	8.91	10.34	13.90
Slopes	12.94	9.34	20.37	5.81	13.43	17.61	7.10	8.75
Waterlogged plateaus	0.35	0.13	0.20	0.72	0.03	0.45	0.64	0.92
Valleys	7.17	11.83	6.89	7.66	6.83	7.94	5.46	5.53
Highlands	14.08	10.98	14.61	8.22	18.16	11.03	6.61	7.73
Broken highlands	0.37	1.31	0.29	0.69	0.18	0.88	0.03	0.14
Broken mountains	0.05	0.04	0.16	0.02	0.18	0.48	0.00	0.01
Ridges	3.67	3.09	7.02	1.23	3.84	2.03	1.06	0.48

Table 2: Proportion of bedrock types at damaged areas and in relic tree-species stands

Bedrock	Clear-cuts	Dead forest	*Picea*	*Pinus*	*Larix*	*Betula*	*Salix*	*Populus*
Limestones	0.18	0.15	0.14	0.23	0.45	0.07	0.52	0.23
Marls	0.98	0.82	0.63	1.50	1.54	2.14	2.69	3.19
Marl flysch	2.50	1.18	3.11	1.92	4.22	2.58	6.18	2.30
Spongilities	2.20	1.17	3.08	3.33	5.75	2.69	1.29	1.93
Loess	1.68	1.15	0.89	2.51	2.04	3.92	8.88	7.63
Lime sandstone	0.39	0.44	0.25	1.90	0.51	1.31	0.85	1.22
Serpentinites	0.16	0.17	0.08	0.34	0.11	0.02	0.05	0.03
Alkaline young volcanites	0.99	0.95	1.27	0.83	3.79	3.03	2.97	4.12
Alkaline crystallinicum	1.71	1.10	1.92	1.28	1.74	1.19	1.02	1.34
Sandstone flysch	4.61	4.07	3.54	0.79	2.35	1.60	1.25	0.97
Neutral perm	1.98	2.30	2.15	3.04	3.13	2.49	1.60	3.43
Graywackes	14.89	10.21	10.07	9.81	19.60	7.00	5.21	5.42
Loamy gravel-sands	1.17	0.53	0.58	3.69	1.62	3.17	4.46	4.37
Neutral young volcanites	0.43	0.33	0.62	0.46	1.42	0.99	0.17	0.28
Neutral plutonits	7.64	12.29	5.38	7.26	4.76	3.21	2.97	4.61
Various metamophites	5.75	6.45	6.12	3.87	5.20	4.23	4.02	3.72
Acid plutonites	7.55	6.70	10.00	7.59	5.93	7.91	2.42	4.56
Acid metamophites	30.14	36.28	33.88	18.61	22.16	29.36	11.13	17.78
Cherts	1.65	1.30	2.25	1.34	3.56	1.07	0.10	0.35
Gravel-sands	0.93	0.47	0.31	4.33	0.41	1.60	0.30	1.29
Eolian sands	0.55	0.37	0.02	2.63	0.12	0.96	0.50	0.95
Block sandstones	2.85	5.25	2.74	10.07	4.42	7.48	0.58	2.22
Kaolinite perm	0.48	0.13	0.45	3.74	1.05	0.76	0.40	0.75
Alkaline waterlogged sediments	0.28	0.09	0.23	0.34	0.15	0.45	2.22	2.82
Cumulated floodplain sediments	0.01	0.00	0.00	0.01	0.00	0.00	7.68	1.84

Bedrock	Clear-cuts	Dead forest	*Picea*	*Pinus*	*Larix*	*Betula*	*Salix*	*Populus*
Loamy floodplain sediments	0.30	0.08	0.06	0.16	0.06	0.33	16.69	10.38
Stony floodplain sediments	0.08	0.01	0.02	0.01	0.01	0.04	8.02	2.18
Acid waterlogged sediments	7.01	5.30	7.66	7.10	3.47	7.34	4.96	9.02
Peaty sediments	0.77	0.53	1.85	1.19	0.39	2.41	0.54	0.57
Wetlands	0.00	0.00	0.00	0.01	0.00	0.02	0.33	0.47
Moorlands	0.13	0.17	0.69	0.12	0.03	0.64	0.00	0.01

Regression models

Conditions at clear-cuttings were significantly more similar to those at mixed forests than dead forests or pure heliophilous stands, while abandoned dead forests were more similar to pure heliophilous stands than clear-cut stands. At least 50 % of the area impacted by bark-beetles was suitable for pine, and 73 % of the area for European larch. Likewise, 50 % of clear-cuttings were suitable for admixed birches, 74 % for admixed conifers and 81 % for admixed spruce. In comparison, 60 % of dead forests were suitable for admixed spruce and 64 % for admixed pine (Table 3).

All logistic regressions were characteristic by positive direction with a negative asymptote, suggesting direct proportionality between damaged stands and heliophilous trees. Overall, regression directions for pure spruce and pine stands were lower than those for mixed stands, while those for pure larch and broadleaved stands were higher than those of mixed stands. Similarly, regressions between clear-cuttings and mixed conifer stands were typically lower than those for dead forests. Finally, regressions for clear-cuttings with a mixed occurrence of heliophilous broadleaved trees were higher than those for dead stands (Table 4).

Forest dieback and heliophilous trees were statistically similar six growth condition types. The largest range and all growth condition types under damage have included simultaneously mixed spruce stands on 38.93 % from afflicted soils. Broken greywacke plateaus (B-M) formed sites of eight from nine assessed stand types similar to conditions of culminating bark-beetle impact. Sites suitable for mixed spruce stands were situated on acid metamorphites (B-S), highland acid metamorphites (V-S), hillycountry acid metamorphites (P-S), slope acid metamorphites (S-S) and depressions with acid waterlogged sediments (D-AWS), but not B-M. Conditions for pure spruce stands corresponded with 34.9 % from afflicted soils.

Fig. 4: Logistic regressions between damaged sites and sites with relic tree-species suitable for pure stands

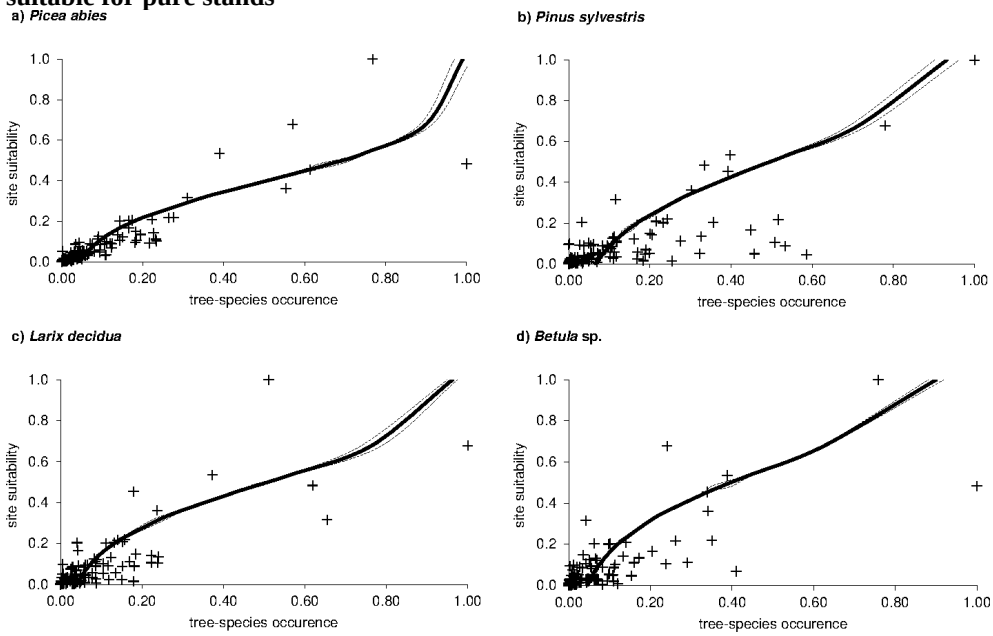


Table 3: Dependence proximity between proportion of damaged geomorphological-bedrock bodies and relic tree-species stands through linear and logistic regressions

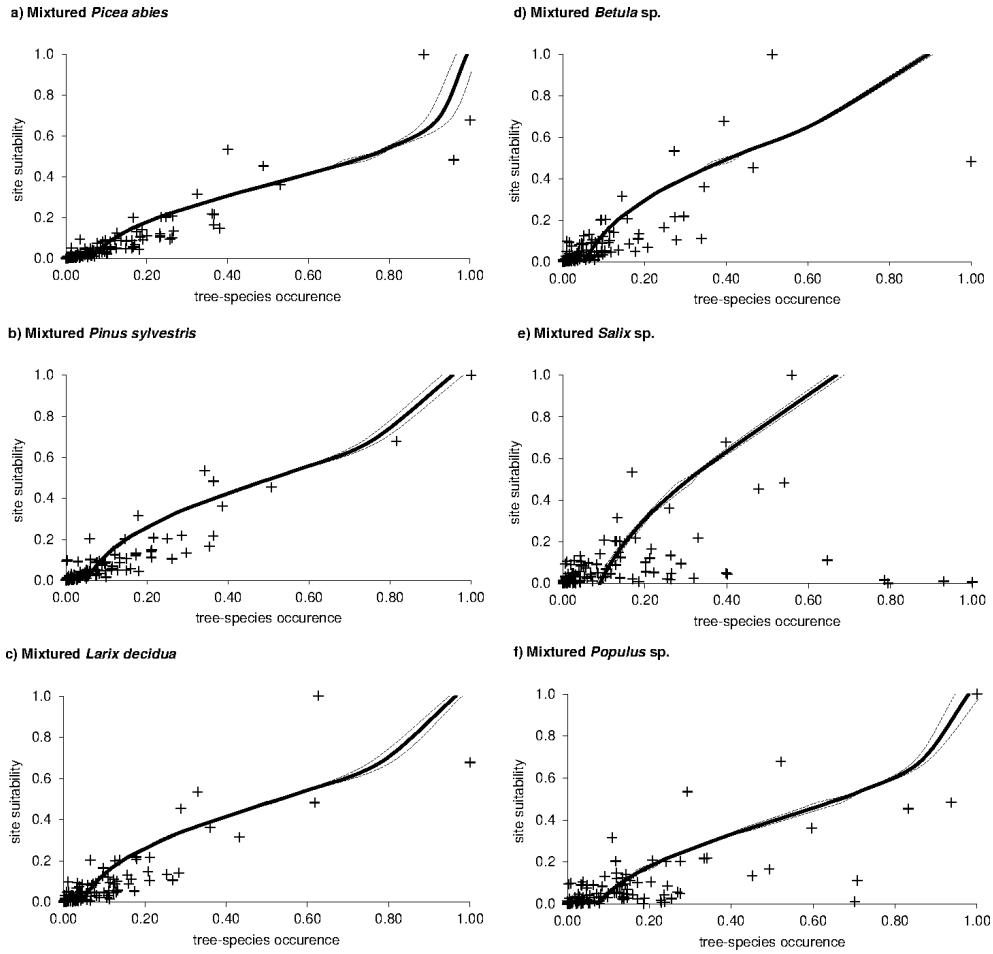
Compound		Linear regression					Logistic regression				
Site	Tree	total	conserved	pure	dominant	admixed	total	conserved	pure	dominant	admixed
Clear-cut	*Picea*	**0.77**	0.24	**0.66**	**0.81**	**0.84**	**0.70**	0.14	**0.55**	**0.77**	**0.81**
	Pinus	**0.63**	0.05	0.32	**0.60**	**0.87**	**0.57**	**0.57**	0.28	**0.54**	**0.80**
	Larix	**0.76**	0.38	**0.61**	**0.67**	**0.77**	**0.73**	**0.73**	**0.64**	**0.64**	**0.74**
	Betula	**0.58**	-	**0.61**	0.49	**0.61**	0.45	-	**0.53**	0.36	**0.50**
	Salix	0.06	-	0.01	0.03	0.14	0.06	-	0.01	0.03	0.13
	Populus	0.36	-	0.08	0.24	**0.56**	0.34	-	0.09	0.22	**0.53**
Dead	*Picea*	**0.56**	0.15	0.49	**0.59**	**0.61**	0.45	0.08	0.36	**0.51**	**0.60**
	Pinus	**0.56**	0.05	0.31	**0.53**	**0.73**	**0.50**	**0.50**	0.27	0.47	**0.64**
	Larix	**0.50**	0.30	0.46	0.42	**0.51**	0.42	0.42	0.49	0.32	0.42
	Betula	0.42	-	**0.51**	0.36	0.43	0.28	-	0.43	0.23	0.29
	Salix	0.04	-	0.00	0.02	0.10	0.04	-	0.00	0.02	0.09
	Populus	0.28	-	0.06	0.18	0.43	0.25	-	0.07	0.17	0.39
Total	*Picea*	**0.56**	0.15	0.49	**0.59**	**0.61**	0.45	0.08	0.36	**0.51**	**0.60**
	Pinus	**0.56**	0.05	0.31	**0.53**	**0.73**	**0.50**	**0.50**	0.27	0.47	**0.64**
	Larix	**0.51**	0.30	0.46	0.42	**0.51**	0.42	0.42	0.49	0.32	0.42
	Betula	0.42	-	**0.51**	0.36	0.43	0.28	-	0.43	0.23	0.29
	Salix	0.04	-	0.00	0.02	0.10	0.04	-	0.00	0.02	0.09
	Populus	0.28	-	0.06	0.18	0.43	0.25	-	0.07	0.17	0.39

Table 4: Regression parameters of dependences between damaged geomorphological-bedrock bodies and relic tree-species stands

Compound		direction (a)					asymptote (b)				
Site	Tree	total	conserved	pure	dominant	admixed	total	conserved	pure	dominant	admixed
Clear-cut	*Picea*	7.15	2.71	6.23	7.79	7.64	-3.18	-3.20	-3.26	-3.09	-2.76
	Pinus	5.28	1.90	4.26	5.25	5.99	-2.67	-3.19	-2.57	-2.65	-2.95
	Larix	6.46	5.87	7.91	6.41	6.39	-3.08	-2.49	-3.09	-3.18	-3.07
	Betula	4.43	-	5.24	3.76	5.02	-2.95	-	-3.04	-3.12	-2.88
	Salix	2.38	-	1.49	2.04	3.02	-2.53	-	-3.00	-2.80	-2.32
	Populus	4.41	-	2.60	3.44	6.44	-2.56	-	-3.05	-2.78	-2.54
Dead	*Picea*	6.68	2.29	5.18	8.19	9.81	-2.89	-3.15	-2.99	-2.85	-2.69
	Pinus	6.54	1.74	5.31	6.46	7.11	-2.60	-3.13	-2.52	-2.56	-2.81
	Larix	7.08	8.24	8.93	6.30	6.93	-2.87	-2.51	-2.94	-2.88	-2.84
	Betula	3.57	-	5.37	3.27	3.75	-2.79	-	-2.90	-3.03	-2.66
	Salix	2.18	-	1.36	1.93	2.70	-2.46	-	-2.96	-2.75	-2.23
	Populus	4.14	-	2.48	3.25	6.97	-2.42	-	-2.98	-2.68	-2.38
Total	*Picea*	6.69	2.29	5.19	8.19	9.81	-2.89	-3.15	-2.99	-2.85	-2.70
	Pinus	6.54	1.74	5.31	6.47	7.12	-2.60	-3.13	-2.52	-2.56	-2.81
	Larix	7.08	8.24	8.94	6.32	6.94	-2.87	-2.51	-2.94	-2.89	-2.85
	Betula	3.57	-	5.38	3.27	3.75	-2.79	-	-2.90	-3.03	-2.66
	Salix	2.18	-	1.36	1.93	2.70	-2.46	-	-2.96	-2.75	-2.23
	Populus	4.15	-	2.48	3.25	6.97	-2.42	-	-2.98	-2.68	-2.38

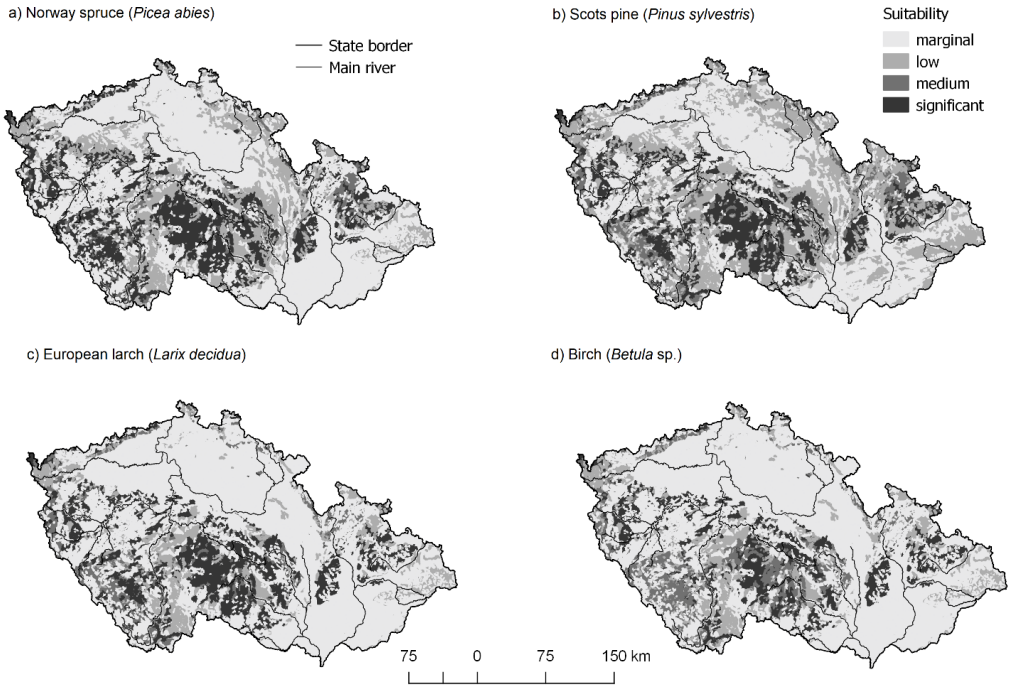
Pure pine and mixed pine stands occurred on the same three bodies B-M, B-S and P-S at 28.0 % for both proportions from damaged forests. Birch stands occurred on the same two growth condition types B-M and B-S as damaged forests too (Fig. 4–5).

Fig. 5: Logistic regressions between damaged sites and sites with relic tree-species suitable for mixed stands



There were significant similarities between pure and mixed stands with afflicted growth conditions have occurred for all heliophilous trees investigated at same parts of the Hercynian subprovince. Conditions allowing the spread of pure heliohilous stands after bark-beetle attack occurred most often in the east and south of the CR from the Low Jeseník Mts. across the Drahany Highlands to the Bohemian-Moravian Highland, the Bohemian Forest Foothills, the Plzeň Hillycountry and the Slavkov Forest (Fig. 6).

Fig. 6: Distribution of geomorphological-bedrock bodies differently suitable for pure relic tree-species stands



Only in the Bohemian Forest Foothills conditions appear less suitable for the spread of birch. The conditions S-S (7.25 %), B-S (4.99 %) and D-AWS (4.31 %) included the most significant sites for pure conifer stand spreading. The broadleaved stands can occupy larger areas on same bedrock types being less suitable along the Hercynian subprovince margins. Mixed stands can cover 64.42 % of same conditions, while pure stands just 35.6 %. Only S-S (29.22 %) and B-S (23.11 %) have included more than a half from conditions suitable for the spread of mixed forest following bark-beetle attack (Fig. 7).

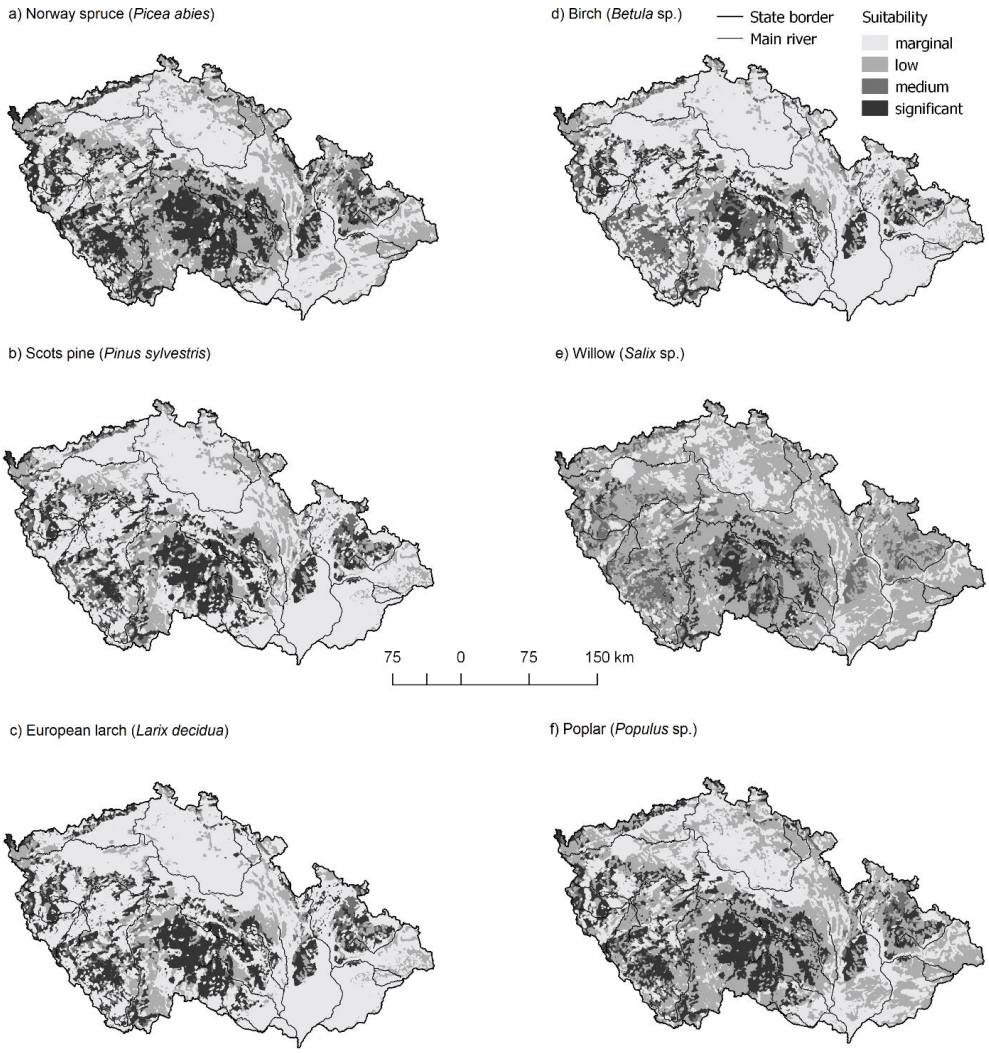
DISCUSSION

Culminating forest dieback on territory of the Czech Republic have cleared sites for mixed heliophilous tree stands. The most suitable clear sites occured at flat reliefs with acid bedrock. Similarities between sites of dead forests and heliophilous trees suggested course of ecosystem restoration preserving glacial species.

Forest sites for heliophilous trees have been cleared due to distrurbances. The climate change effects on increasing disturbance frequency raises proportion of heliophilous trees (Hlásný *et al*., 2011). In contrast, the sites cleared more frequently complicate growing up of long-live woods (Konôpka *et al*., 2008). The abrupt dieback in the CR opened sites suitable for return of Norway spruce, Scots pine, European larch, birches and poplars. Dead forests have concentrated at conditions similar more for mixed stands than for homogenous stands. On the other hand, the conifer sites were similar to severe damaged areas more than sites of

heliophilous broadleaved trees. The occurences of mixed poplar floodplains were more similar with character of cleared sites than conditions for birches.

Fig. 7: Distribution of geomorphological-bedrcok bodies differently suitable for mixed relic tree-species stands



Post-disturbance forest ecosystem restoration is driven by both competitions between individual heliophilous tree-species and by the penetration rate of long-live heliophobic species. Courses toward forest restoration focused on encouranging a heliophilous tree canopy as protective cover for heliophobic trees on one hand, and on planting sufficiently resistant species on the other (Walentowski *et al.*, 2017). Demands for continual timber production tend forestry to favour fast-growing resistant tree-species, which will provide sufficient wood mass until any impact from another disturbance (Pommering & Murphy, 2004). A continuous decline in both spruce and pine stock increment due to climate change

suggests that use of either species for providing temporary cover to incoming heliophobic trees would be unsustainable (Treml *et al*., 2022).

The economic needs are imperfectly intertwined with condition range suitable for heliophilous trees. The greatest similarities between heliophilous trees stands and abruptly afflicted submountain sites were found on greywackes, acid metamorphites and waterlogged sediments. Poor or waterlogged soils are suitable for permanent conifer presence (Douda *et al.*, 2015). However, the indication of the natural conifer occurrence in submountain altitudes assessed through site similarity is inaccurate, as indigenous conifer distribution under Central-European conditions has been impacted by economic forest conversion (Pretzsch *et al*., 2014). In contrast, the occurrence of deciduous trees has remained within their natural growth condition range. Though heliophilous trees are similarly tolerant to different soil properties, they achieve highest production on nutrient-rich sites (Souček *et al*., 2016). For this reason, the economic demands for high timber production rates limit natural regeneration of glacial refugia to poorer soils.

Consequently, protection of glacial refugia and provision of an economically profitable forest composition seems to be achievable through spatially distributed extraction of ecosystem benefits. Such benefits are stable as long as requirements for tree growth and soil are maintained. The requirements between tree-species and soil develop either through natural regeneration or through transfer within conditions of natural distribution (Lindner *et al*., 2010).

Broadleaved trees are more important for forest adaptation to climate change respecting growth requirements due to preservation of their natural distribution range, despite these mainly being found in growth conditions less similar to those afflicted by abrupt dieback. The conserved forests were only sporadically damaged as their growth conditions were less similar to those in the dieback. Dieback in protected spruce or pine forests occurred mostly on outcrops of block sandstones or in limestone valleys, which were neither dominantly afflicted sites nor significantly similar to areas with heliophilous broadleaved trees (Elznicová *et al*., 2012).

Spatial differentiation of benefits accrued from forests, based on correlations between tree-species and site, prevents large-area disaster (Pommerening & Grabarnik, 2019). Naturally dominant broadleaved trees and suitable conditions for conifers at submountain altitudes of the CR have confirmed that mixed forests do indeed reduce ecosystem collapse threats. The differences between growth conditions in broadleaved tree and dead forests were suggestive of natural competetive differentiation to ecosystem adaptation. The increased similarity between dead forest conditions and submountain floodplains have distinguished potential distribution of poplar or willow communities. Floodplain communities allowed an irreplaceably rapid spread of biota during the Quaternary environmental changes. They simultaneously provided habitats for survival of termophilous vegetation, which was then able to quickly colonise tundra at the end of the ice ages (Wagner *et al*., 2021). Despite this, large submountain areas that have been left to natural regeneration are often overgrown with rare tree-species, which increase biodiversity markedly (Machar, 2012). The increased biodiversity in mixed forests subsequently drives adaptation to environmental change (Kanevskiy *et al*., 2022). As a result, forest biodiversity optimised to soil represents an important tool for simultaneously protecting glacial species and ensuring stable timber production.

CONCLUSION

Forest dieback following extraordinarily dry seasons have cleared sites suitable for mixed stands of relic Norway spruce, Scots pine, European larch, poplars and birches on acid bedrocks at altitudes, where temperate broadleaved trees naturally dominate. Clear-cuttings have provided more suitable sites than dead forests. The best conditions for temporal occurrence of heliophilous relic species were provided on broken greywacke plateaus, acid metamorphites and waterlogged sediments. The differentation in proportion of heliophilous tree-species seems as fundamental for correlation between relic tree conservation and stable wood mass production. The correlation of tree compostion with growth conditions provides a tool for sustainable adaptation during the restoration of forests subjected to abrupt dieback due to climate change.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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