Ann. For. Res. 56(2): 317-338, 2013

ANNALS OF FOREST RESEARCH
www.e-afr.org

Beech bark necrosis: partitioning the environmental and spatial variation of the damage severity in Central and South-Eastern Europe

B. Jarčuška, I. Mihál, A. Cicák, H. Tsakov

Jarčuška B., Mihál I., Cicák A., Tsakov H., 2013. Beech bark necrosis: partitioning the environmental and spatial variation of the damage severity in Central and South-Eastern Europe. Ann. For. Res. 56(2): 317-338, 2013.

Abstract. The beech bark necrosis (BBN) infestation severity of European beech (*Fagus sylvatica* L.) was assessed in regions of Central (CE) and South-Eastern Europe (SE). Altogether more than 10,000 trees were sampled at 114 sites. Using variation partitioning method, we examined the pure and shared effects of stand, site, climate and spatial sets of variables on mean BBN severity. Our rating included (i) the whole stand, (ii) tree social status classes, (iii) canopy (C) and (iv) understory (U) trees separately. We found that C trees were less affected by BBN than sub-canopy and U trees in both regions. There were found inter-regional differences in amount of explained variability (25.4–73.9%) for whole stand BBN and in the sensitivity of C and U trees to the environmental gradients. The analysis revealed that the climate and spatial variables followed by stand variables had the largest marginal effects on mean BBN severity in all models, while the site set of variables had the weakest one. More than half of the explained variation was shared among four sets of variables in SE, contrary to CE. Except to U trees in SE, the effect of climate – pure or spatially structured – remained the highest also after partitioning of variance; more in SE than in CE. Taking into account positive association between mean annual temperature and mean BBN severity in C trees in SE, reinforced negative effect of climate change on the necrosis might be expected to be more serious mainly in low situated beech forests there. Promoting the tree species diversity in forested areas with higher incidence of beech bark necrosis, i.e. in low altitudes in SE, could reduce the susceptibility of forests to the necrosis at regional level in the future. For better understanding of the relative importance of environmental and spatial variables on BBN severity, further research performed on finer spatial scale (extent and grain) is necessary, along with accounting for pathogens involved in the infestation.
Keywords variation partitioning, *Fagus sylvatica*, bark necrosis, environment, spatial variability.

Authors. Benjamín Jarčuška (benjamin.jarcuska@gmail.com), Ivan Mihál, Alojz Cicák - Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, 960 53 Zvolen, Slovakia; Hristo Tsakov - Forest Research Institute, Bulgarian Academy of Sciences, 132, St. Kliment Ohridski, Blvd. 1756, Sofia, Bulgaria.
Manuscript rreceived August 08, 2013; revised November 15, 2013; accepted November 18, 2013; online first November 25, 2013.

Introduction

European beech (*Fagus sylvatica* L.) is a broadly distributed European tree species, what is reflected in its high ecological and economic importance (Packham et al. 2012). Its importance can be expected to rise in the future as a prerequisite for mitigation of impacts of predicted climate change on forest ecosystems, e.g. as improving the stability of forest ecosystems (Knoke et al. 2008, Bolte et al. 2009).

Value of the species as stabilizing constituent of the ecosystems against the climate change depends on health status of trees. The most common health problems of European beech are associated with necrotic bark damage (Jung 2009). Necrotic damage of beech bark tissues is associated with activity or interaction among various fungal and insect pathogens, mainly fungi of genus *Anthostoma* Nitschke, *Cytospora* Ehr.: Fr., *Diatrype* Fr., *Fusarium* Link., *Nectria* (Fr.) Fr., *Ophiostoma* Syd., *Phytophthora* de Bary, *Phomopsis* Sacc., *Valsa* Fr., *Verticillium* Nees., etc. (Houston 1994, Jančařík 2000, Jung 2009, Merezhko et al. 1994, Mihál et al. 2009, Perrin 1984). The bark necrosis is of noticeable economic and ecological importance, particularly in North America ("beech bark disease" complex: ascomycetous fungus (*Neo*)*nectria* sp. with beech lice *Cryptoccocus* sp.; Houston 1994). Similarly, in some European countries increasing number of stands is declining during past years (*Phytophthora* diseases, Jung 2009; see also Jančařík 2000, Mihál 2002, Mihál et al. 1998, Surovec 1990). Negative effect of beech stem bark necrosis on tree's health status may be subsequently reflected in stand vitality, ecosystem stability and in commercial utilization of timber.

Environment is an important, but often overlooked factor in disease severity in plants by affecting the relationship between the host plant and pathogen (Wolinska & King, 2009, Sturrock et al. 2011). Various biotic and abiotic components of the environment alter the fitness of hosts and pathogens, and consequently each environmental variable might be either beneficial or detrimental for plant health (Scholthof 2007). The environmental control of the plant-pathogen interrelationship can be integrated into the disease triangle, a classic plant pathology concept examining the role of the environment in disease processes across-plant life-history (Scholthof 2007, Vale et al. 2011). Recognizing the effects of environmental factors on host-pathogen relationship could improve our understanding on the management of diseases (Holdenrieder et al. 2004, Allen et al. 2010, Sturrock et al. 2011), esspecially in the context of climate change (Dukes et al. 2009, Anderegg et al. 2012).

In this study we explore the effects of some environmental determinants (stand, site and climate variables) on the severity of beech bark necrosis (BBN) at stand and canopy layer level. We investigated whether the patterns observed for whole stands hold when considering the social status of trees within the canopy (i.e. for canopy and understory trees). The canopy and understory trees may be expected to show differences in BBN patterns, as relationship between environment and the tree stress response is changed during the tree ontogeny (Niinemets 2010). Firstly, we identified environmental variables accounting for a major part of BBN variability, from a larger set of variables. These parsimonious variables were used further for building models explaining the variance of dependent variables – the mean BBN severity of various levels of canopy structure. The analysis was conducted for two European regions: Central and South-Eastern Europe.

Material and methods

Study area and sites

The study was performed in two European

regions: Central Europe (CE) - in Slovakia, Czech Republic, Poland, Hungary and Romania, and South-Eastern Europe (SE), in Bulgaria and Serbia (Fig. 1). According to Köppen-Geiger climate classification, most of CE belongs to the continental climate zone, while SE lies between the oceanic and continental climatic zones, and is adjacent to the zone of Mediterranean climate (Peel et al. 2007). Moreover, there are differences in quaternary history of European beech between these regions (Magri et al. 2006).

Altogether 114 forest stands and 10,309 trees were inspected from 1995 to 2011(68 stands, 7879 trees, mode = 100 per stand in CE and 46 stands, 2430 trees, mode = 50 per stand in SE).

The selection of sites aimed to capture the altitudinal gradient in beech occurrence across the two studied regions. Some of these sites served in inventory assessments of the health status of beech forests within selected regions (Cicák & Mihál 1997, 2008, Cicák et al. 2006), while other were located on permanent research plots. The study sites elevation was between 300 to 1550 m a.s.l. The mean annual temperature ranged from 3.5 to 12.3 °C, while the mean annual precipitation varied between 568 to 1137 mm (Hijmans et al. 2005). In both regions, the sites differed in most climate characteristics used as explanatory variables in this study (Table A1 - tables and figures with an A before number are in Appendix).

Data collection

In a site, an approximately square plot was placed along the contour line and in each CE and SE sites, 100 and 50 trees were measured, respectively. Accordingly, size of the plot was related to the stand density. In some permanent research plots (7 sites in CE, and 17 in SE), the number of measured trees was equal to the number of trees of individual permanent research plot.

Explained variables: the beech bark necrosis. At each site, for each beech tree, we rated the severity of bark necrosis and tree so-

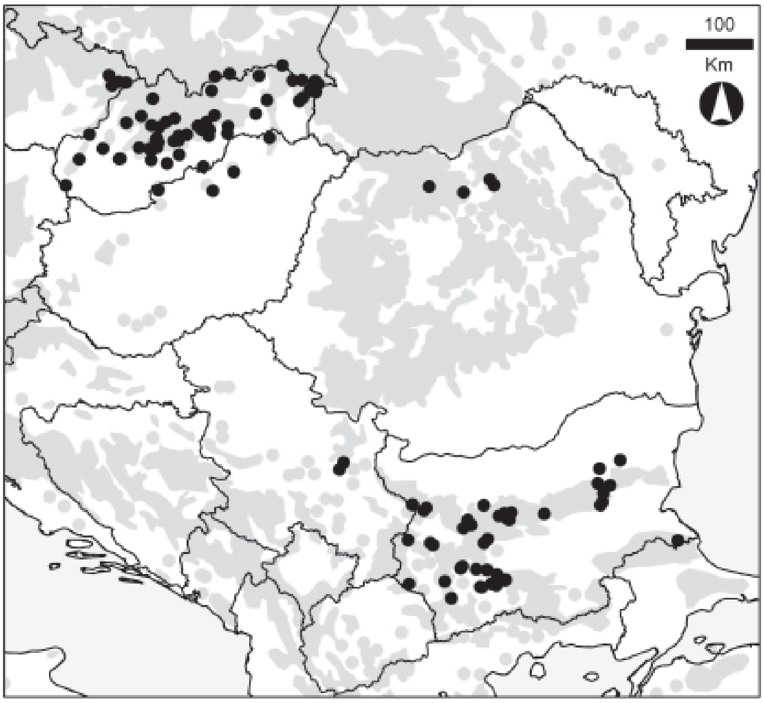

Figure 1 Location of the studied localities within the eastern part of the Europe and the distribution of European beech (*Fagus sylvatica* L.)(source: EUFORGEN, http://www.euforgen.org).

cial status. For a tree stem (up to crown base), the severity of bark infestation was rated on an ordinal scale (Table 1, Fig. A1, according to Cicák & Mihál 1997). Each observed tree was assigned to one of the three canopy layers, according to its relative height: (i) canopy trees – the tallest trees in the forest stand, with crowns forming the uppermost layer, (ii) subcanopy trees – trees smaller than those in the canopy, partially shaded by canopy trees, with crowns often suppressed, with top of the crown reaching the bottom of the stand canopy, (iii) understory trees with reduced and completely shaded crowns, reaching maximum height of c. ½ of canopy trees and of minimal diameter at breast height of 6 cm.

At stand level, the mean BBN severity rating was calculated by averaging the stand level data of the BBN ranks for each tree (as arithmetic mean of all trees sampled within each stand). The same procedure was followed in the case of canopy layers, i.e. the three social status classes.

Explanatory variables: stand, site, climate and spatial. Altogether 29 variables were considered to explain the severity of BBN infestation in the present study: four stand variables, three site variables, 14 spatial and 8 climate variables.

The stand characteristics – abundance of beech, stand age and stocking (stand density, i.e. ratio of real and model tree basal area) – were taken from present forest management plans. Stand structure was expressed as percentage of understory trees from all sampled trees within stand.

Site parameters – curvature, slope and potential solar radiation – were derived from a digital elevation model with resolution of 30 m (ASTER GDEM V2 2011; MESI, Japan; NASA, USA), using ArcGIS 10 software (ESRI, USA) and Spatial Analyst toolbox. The surface curvature was calculated cell by cell as the two dimensional second derivative of the surface slope from the elevation values of the analyzed cell and its eight immediate neighbors. A positive curvature indicates that the surface is upwardly convex at that cell; a negative curvature indicates that the surface is upwardly concave at that cell (ESRI 2011). Potential point solar radiation was calculated for a period of whole year for both regions separately.

Seven of eight climate characteristics employed in the study were compiled from the WorldClim current climate dataset (Hijmans et al. 2005; www.worldclim.org). WorldClim maps are derived from monthly values gathered from thousands of weather stations around the world between 1950 and 2000 (c. 50,000 locations for precipitation and c. 25,000 locations for temperature).

The climate characteristics were chosen based on known relationships with "beech bark disease" severity. For example, it is known that drought stress (Jung 2009, Kasson & Living-

Table 1 Characteristics of ordinal rating scale for beech bark disease severity on stems of European beech

Rating	Characteristics
0	without any necrotic wounds on the bark
1	small necrotic wounds (bark fissures, cracks) occurring singularly or in individual groups, visible only with closer examination of the stem
2	small necrotic wounds (as for the degree 1) accompanied by occurrence of larger necrotic wounds (larger fissures, rugged bark) visibly under ordinary examination of the stem
3	larger necrotic wounds denuding the xylem and partly deforming the stem, bark cracking and shedding, visible already from a larger distance
4	large necrotic wounds deforming the stem heavily or leading to "bark necrosis", rugged bark and bark shedding, visible also from greater distance

Note. See Fig. A1 for a visual representation of particular degrees ston 2012), and low air temperature (below -37 °C; Griffin et al. 2003, Kasson & Livingston 2012) are associated with "beech bark disease" infestation. The climate data were provided in a GIS-based raster format, with a spatial resolution of c. 1 km^2. Seven bioclimatic variables were used: mean annual temperature, temperature seasonality, minimum temperature of coldest month, mean temperature of driest quarter, annual precipitation, precipitation seasonality, and precipitation of driest quarter. The altitude was attached to this set of characteristics due its close association with temperature and precipitations; it was directly read out from forestry maps during the field work. Table 2 presents the variables abbreviations, units and descriptions.

Spatial patterns of BBN severity were assessed through variables derived from geographic coordinates of each stand, fitted by a cubic trend surface. There were used these derived spatial variables: x, y, x^2, y^2, x^3, y^3, xy, x^2y, x^3y, xy^2, xy^3, x^2y^2, x^2y^3 and x^3y^3 (where x = latitude, and y = longitude), thus, 13 variables were considered. This ensures not only the distinction of the linear gradient patterns in the explained data, but also complex broad-scale features, like patches and gaps (Borcard et al. 1992, Borcard & Legendre 2002).

Data analyses

Significance of between-regional differences in the mean BBN rating of stand and tree social classes were tested by Mann-Whitney U test, while the differences among the three canopy layers within a region with Friedman ANOVA, followed by Wilcoxon Matched Pairs post-hoc tests.

After examining the scatter plots of mean BBN rating vs. explanatory variables for linearity, we applied redundancy analysis (RDA) in order to examine the relationships among the mean BBN infestation severity and explanatory variables. The RDA technique is known as a constrained ordination method assuming a linear response of explained variables (ter Braak & Šmilauer 2002). Prior to analysis, all the variables (Table 1) were centered and standardized to a mean of zero and a variance of one. We performed separate analyses for both the regions. For a particular region, we performed four sets of RDAs, considering as dependent variables each of: (i) the mean BBN rating of the whole stand, (ii) the mean BBN ratings of tree social classes, (iii) the mean BBN rating of canopy trees, and (iv) the mean BBN rating of understory trees (Table 1). For analysis of the mean BBN rating of the whole stand, we used the data from all sites (n = 68 and 46 for CE and SE, respectively), while for the other analyses sites with all tree social classes (CE - 62 and SE - 25 sites) were used.

In order to identify the most parsimonious set of variables within each set of explanatory variables, firstly we performed a forward selection procedure by using CANOCO 4.5 (Microcomputer Power, USA, ter Braak & Šmilauer 2002). With respect to the exploratory character of the study, all the variables with a probability $P < 0.10$ in the selection procedure were kept for building the models. Statistical significance of each added variable and the subsequently developed model was tested using an unrestricted Monte Carlo permutation test with 9,999 permutations. Such models represented the marginal fractions of variance explained by the relevant sets of explanatory variables (the marginal effect). The marginal fraction is the partition of variance explained when a set of explanatory variables is used alone, i.e. without covariables, in the analysis. The resulting sets of explanatory variables selected in the previous step were further used to compute the total explained variation of explained variable(s), and in variation partitioning. The final step was variation partitioning using partial RDAs (Borcard et al. 1992, Lepš & Šmilauer 2003). This was viewed as an exploratory tool (see Gillbert & Bennett 2010), to determine the relative contributions of each set of variables, alone or in combination (interaction). The partitioning

Table 2 Variables used in the study

Variable	Abbre-viation	Description	Data source
Explained variables			
Whole stand			
Stand's necrosis severity	S	Mean beech bark necrosis severity rating of whole stand	Visual estimates and calculation*
Canopy layer			
Canopy trees' necrosis severity	C	Mean beech bark necrosis severity rating of canopy trees	Visual estimates and calculation*
Sub-canopy trees' necrosis severity	S-C	Mean beech bark necrosis severity rating of sub-canopy trees	Visual estimates and calculation*
Understory trees' necrosis severity	U	Mean beech bark necrosis severity rating of understory trees	Visual estimates and calculation*
Explanatory variables			
Stand characteristics			
Beech abundance	abun	Relative abundance of beech in the stand	Forest management plans
Stand age	age	mean age of trees in canopy layer	Age of canopy trees
Stand structure	struct		Calculation*
Stocking	stock	Ratio of real and model tree bazal area	Forest management plans
Site characteristics			
Potential solar radiation	rad	Point solar insolation (Wh m^{-2} $year^{-1}$)	Derived from DEM
Slope	slope	Relief slope (°)	Derived from DEM
Overall surface curvature	curv	(unitless)*	Derived from DEM
*Spatial characteristics**			
Latitude	N	Geographic position	GPS
Longitude	E	Geographic position	GPS
Climatic charactics			
Altitude	alt	Stand elevation (m a.s.l.)	Forestry maps of stands
Annual mean temperature	MAT	(°C)	WordClim (Hijmans et al. 2005)
Temperature seasonality	TS	standard deviation of monthly means (°C)	WordClim (Hijmans et al. 2005)
Minimum temperature of coldest month	MTCM	(°C)	WordClim (Hijmans et al. 2005)
Mean temperature of driest quarter	MTDQ	(°C)	WordClim (Hijmans et al. 2005)
Annual precipitation	PREC	(mm $year^{-1}$)	WordClim (Hijmans et al. 2005)
Precipitation seasonality	PS	coefficient of variation of monthly values (mm)	WordClim (Hijmans et al. 2005)
Precipitation of driest quarter	PDQ	(mm)	WordClim (Hijmans et al. 2005)

Note. * See Material and methods for details. For descriptive statistics of the variables see Table A1.

assessed the pure effect of a set of variables (pure fraction), thus the percentage variance explained by this set of variables after all statistically significant sets of variables were used as covariables. The joint effect of two or more groups of variables expresses the proportion of variance in which sets of variables cannot be decomposed due to their collinearity. Variance explained is shown as percentage of total inertia. All statistical treatments were performed with software CANOCO 4.5 and Statistica 7 (StatSoft, USA).

Results

Differences between regions and tree social status classes

We found significant differences in the mean BBN severity of stands between the two regions. CE region had more infested stands than SE (mean of 1.12 vs. 0.79; Mann-Whitney U test; z = 4.433; P < 0.0001; two-sided test, n = 68 in CE, n = 46 in SE; Table A1). However, after testing for differences in the mean BBN degree between the tree social classes, we found significant differences between regions only in understory trees (Mann-Whitney U test; z = 3.166; P < 0.0013; two-sided test, n = 62 in CE, n = 25 in SE; Table A1). Thus, within both regions, the severity of BBN was significantly affected by the tree social status (Friedman ANOVA; χ^2 = 93.21; df = 2, 62; P < 0.0001 and χ^2 = 11.04; df = 2, 25; P = 0.004 for CE and SE, respectively). The canopy trees expressed significantly lower BBN severity compared to sub-canopy and/or understory trees. The latter were most affected by BBN in CE (Fig. 2).

Environmental and spatial effects

Whole stand BBN severity. The forward selection procedure selected five variables within three sets of variables from 29 available variables within four sets of variables in CE, and 3 variables in two sets in SE (Table A2).

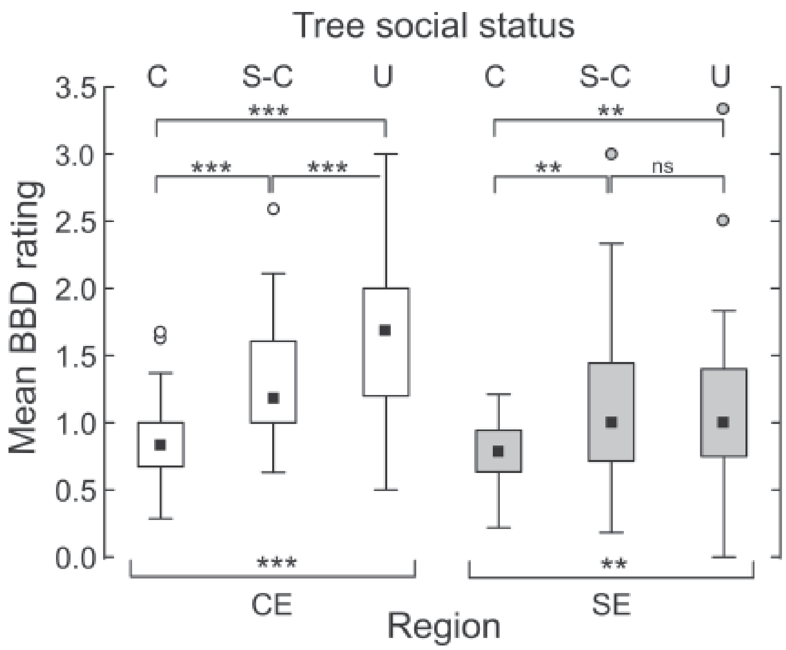

Figure 2 Effect of tree social status on mean beech bark necrosis severity in East-Central Europe (CE) and South-Eastern Europe (SE). Tree classes according the tree social status: canopy (C), sub-canopy (S-C) and understory (U) trees. Differences among the tree classes within region were assessed by Friedman ANOVA followed by Wilcoxon Matched Pairs post-hoc tests. Boxes represent the 25% to 75% quartiles, black squares in the boxes represent the median level, whiskers represent the non-outlier range, and circles represent the outliers.** - P < 0.01, *** - P <0.001 , ns - non-significant

No variables were selected from the site set in CE, and from stand and site set in SE. The selected climate variables as the only constraining variables, explained 22.3% and 41.0% of the variation (i.e. marginal fraction) in the whole stand's mean BBN rating in CE and SE, respectively. Spatial variables accounted for 9.0% and 46.4% of explanatory variable's variance in the two regions, respectively. Subsequently, selected variables together explained 29.1% and 51.2% of the variation in the stand mean BBN rating in CE and SE, respectively (Table A2).

In CE, variation partitioning (Fig. A2) demonstrated that the climate was the most important determinant of the whole stand mean BBN rating. The climate alone (pure effect) explained 16.7%, while stand and spatial variables 6.6% and 0.8%, respectively. Spatially structured was 5.6% of climate variability (Fig. A2). In SE, variation in the stand mean BBN rating explained by climate was mostly spatially structured (36.6%; Fig. A2). Variance explained by pure fractions of spatial variables and climate variables were statistically significant ($P < 0.044$; Table A3).

BBN severity of tree social classes. Taking into account the significant effect of tree social status on mean BBN rating (Fig.2), differences in results of forward selection and/or variation partitioning between models explaining the variance of mean BBN rating of the whole stand and tree social classes could be expected. Forward selection procedure reduced the number of variables to one in stand, one in site, one in spatial and three in climate set in CE, and one in stand, one in site, three in spatial and two in climate set in SE (Table A2). Compared to the analyses at the whole stand level, variables were selected also from site, and site and stand variable sets in CE and SE, respectively (Table A3). The selected variables altogether explained 28.4% and 60.3% of mean BBN rating of 3 tree social classes in CE and SE, respectively (Tables A2-A3; Fig. A2).

In CE, correlation between mean BBN ratings of tree classes was above 0.70 ($P < 0.0001$; Fig. 3A). Ordination of the CE mean BBN rating of canopy, sub-canopy and understory trees constrained by selected variables showed that the sites with strong temperature seasonality (*TS*, on the right side of the RDA-plot; Fig. 3A) had the smallest mean BBN rating of all tree social classes. The sites with the most variable average monthly temperatures during year (*TS*) also had a high yearly variability of precipitations, smaller annual precipitations and were located in the eastern part of the studied region. The sites with abundant annual precipitations (i.e. at high altitudes) had more affected understory trees compared to the sites located on opposite side of the gradient of annual precipitations (Fig. 3A). The mean BBN rating of canopy and sub-canopy trees was negatively associated with the stand age.

In SE, the correlation between mean BBN rating of understory trees and canopy or sub-canopy trees was weaker compared to CE ($R \approx 0.50$, $P < 0.009$; Fig. 3B). Unlike to CE, SE sites with high temperature seasonality and low mean temperature in the driest quarter had canopy and sub-canopy trees with larger mean BBN rating. Canopy and understory trees had large mean BBN rating at sites with small amount of potential solar radiation.

Analogous to the models for the whole stand mean BBN rating, marginal effect of climate variables in CE, and marginal effect of spatial and climate variables in SE, explained the largest proportion of the tree social classes' variability in mean BBN rating (Table A2). The variation partitioning revealed that the only significant pure (partial) effects were stand (5.7%) and climate (10.8%) variables in CE (Fig. A2); no significant pure fractions of four sets of variables were found in SE (Table A3). The largest explained fraction of mean BBN rating's variation (24.8%) was shared between climate and spatial variables in SE (Fig. A2).

BBN severity of canopy and understory trees. After running forward selection separately in each of the four sets of variables, five variables from three sets were retained in models for the CE canopy trees: one stand, one spatial and three climate variables (Table 3). In models for CE understory trees, one variable from site set was retained in addition. In total, the selected variables explained 25.4% and 37.1% of mean BBN severity of CE canopy and understory trees, respectively (Table 3). Six variables selected by forward selection from all sets of variables explained 73.9% of mean BBN rating variability of SE canopy trees, while 5 variables selected from all variables' sets accounted for 54.2% of mean BBN rating variability of understory trees in SE (Table 3).

Climate had the most pronounced marginal effect in CE. However, the only pure fraction significantly explaining variance of mean BBN rating of CE canopy trees was stand fraction (Fig. 4, Table 4). In understory trees, pure fractions of selected stand (5.2%) and climate (14.1%) variables were statistically significant factors, in contrast to the other pure fractions (Table 4). More than 10% of climate variance was spatially structured. As well as in most of other models (6 out of 8; see above), most of the spatial variation was shared with other sets of variables (Fig. 4).

The most important determinant for mean BBN rating in SE canopy trees was climate, followed by spatial and stand variables (Table 4). The variance explained as pure effect of stand and climate variables was statistically significant while the other pure fractions were not. The largest explained fraction was spatially structured fraction of climate (26.7%, Fig. 4). In SE's understory trees, marginal effect of

Table 3 Variance in mean beech bark necrosis severity of canopy trees (Canopy) and understory trees (Understory) explained by stand, site, spatial, and climatic variables retained after forward selection in RDA based on each set of variables (i.e. separately in each set), in East-Central Europe (CE) and South-Eastern Europe (SE)

Variable set	Canopy			Understory		
CE	variable	%	*P*	variable	%	*P*
Stand	age	8.0	0.012	stock	10.0	0.008
Site	-	-	-	curv	5.0	0.084
Spatial	NNE	10.0	0.014	NNNE	15.0	0.002
Climate	TS	7.0	0.037	TS	16.0	0.002
	MTCM	6.0	0.052	MTCM	5.0	0.055
	PREC	5.0	0.064	AnnPrec	8.0	0.011
	Model	17.7	0.011	Model	28.9	0.001
	Total	25.4	0.005	Total	37.1	0.001
SE						
Stand	struct	33.0	0.004	struct	14.0	0.059
				age	11.0	0.092
				Model	25.1	0.041
Site	rad	17.0	0.043	rad	28.0	0.005
Spatial	N	32.0	0.003	NNE	34.0	0.004
	NN	17.0	0.012			
	Model	49.0	0.001			
Climate	TS	45.0	0.001	TS	13.0	0.072
	MTDQ	15.0	0.012			
	Model	59.7	0.001			
	Total	73.9	0.001	Total	54.2	0.007

Note. For the description of variables, see Table 2. Total - variance explained by all variables selected by forward selection in RDA. *P* - significance level; % - ratio of data variability explained by the model.

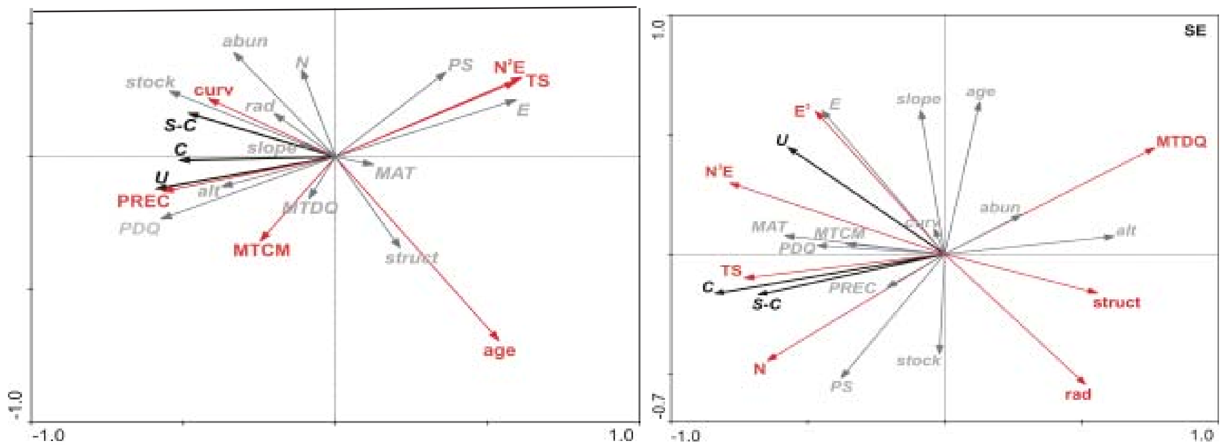

Figure 3 Relationships among explanatory variables and mean beech bark necrosis severity ratings of canopy (C), sub-canopy (S-C) and understory (U) trees (black bold italics) in East-Central Europe (CE) and South-Eastern Europe (SE) visualized in RDA. Explanatory variables selected using forward selection in RDA analyses (Table A2) are in red, other explanatory variables are used as supplementary variables (light gray italics). Selected explanatory variables explained 28.4% and 60.3% of variance of mean beech bark disease severity ratings in CE and SE, respectively. For variables descriptions see Table 2.

climate was non-significant ($P = 0.072$), marginal effect of spatial variance was the biggest one. The only significant pure variable was spatial one (Table 4).

Discussion

Differences between regions and among the tree social status classes

Mean BBD severity rating of whole stand across both regions was 0.99 (range: 0.22–1.97). In other words, an average tree had small necrotic wounds (bark fissures) occurring singularly or in individual groups, visible only with closer examination of the stem (see Table 1, Fig. A1). However, statistically significant differences in beech bark necrosis (BBN) severity between the studied regions were found only in understory trees: CE understory trees were more affected by BBN than SE understory trees. The overall stress sensitivity is expected to be negatively correlated with the tree size. Seedlings and saplings are assumed to be more sensitive to sustained stress events than large non-senescent trees due to smaller carbon reserves of younger growth stages (Niinemets 2010). According to this, in both regions we found the canopy trees less affected by BBN than sub-canopy and understory trees (Fig. 1). Low light availability is typical for understories of forests with closed canopy layer, namely in Europeanbeech forests (van Eimern 1984). Shade-grown plants allocates more biomass in aboveground compartments at expense of roots, therefore these plants may respond more markedly to drought, in comparison with sun-grown plants (Valladares & Pearcy 2002). Moreover, competition with canopy trees in rooting space may strengthen effect of these mechanistic constraints possess by young understory plants (Wagner et al. 2010). Thus, the observed pattern can be associated with filtering out less resistant trees during the ontogeny.

Environmental and spatial patterns of beech bark necrosis

Interaction between a susceptible host plant, a virulent pathogen and a favourable environ-

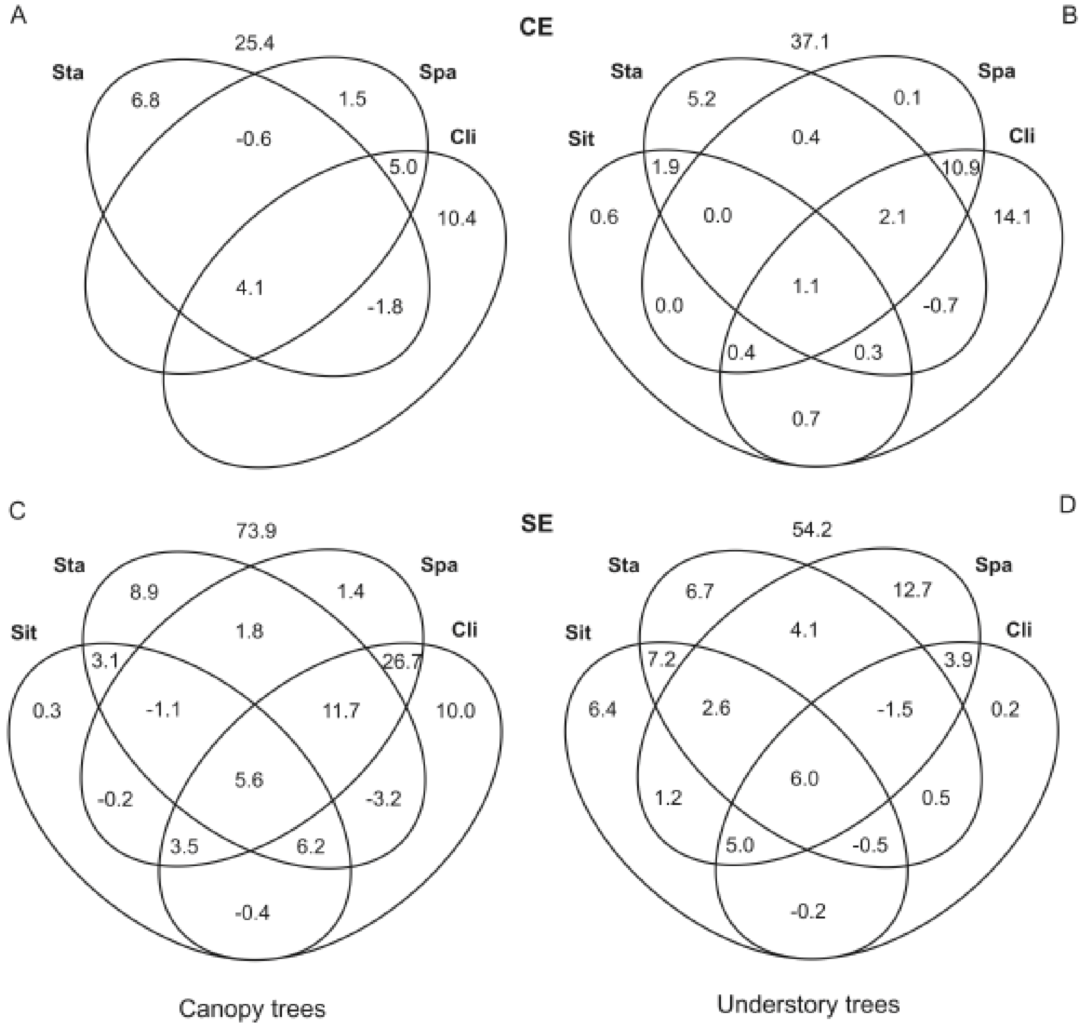

Figure 4 Variation partitioning among stand (*Sta*), site (*Sit*), spatial (*Spa*) and climate (*Cli*) variables for mean beech bark necrosis severity ratings of canopy (A, C) and understory (B, D) trees in East-Central Europe (CE; A, B) and South-Eastern Europe (SE; C, D). Only variables selected by forward selection in RDA analyses (Table 3) were used for variance partitioning. The total variance explained by all variables is above in the Venn diagram. For significance see Table 4

ment results in a plant disease (Sturrock et al. 2011). Factors affecting host-pathogen relationship in complex forest decline diseases (Manion 1991) could be arranged into three sets of mutually interacting factors: predisposing, inciting and contributing (Sturrock et al. 2011). Thus, the sets of stand, site and climate variables used in our analyses (Tab. 2) can be viewed as predisposing factors, as they are long-term, static or slowly changing (Manion 1991, Sturrock et al. 2011). The predisposing factors increase the susceptibility of trees to short-term stresses or to secondary pathogens. The analyses showed that the variables with the largest marginal effects on mean BBN severity were climate and spatial variables followed by stand variables, while site set of variables was the weakest one. This was confirmed for the whole stand, for all tree social status classes, and for canopy and understory trees separately, indicating that these conclusions are robust. However, this should not be interpreted as the evidence that climate exerts a greater influence on mean BBN severity than stand or site vari-

Table 4 Significance of RDA models and variation partitioning among stand, site, spatial, and climatic variables explaining beech bark disease severity of canopy trees (Canopy) and understory trees (Understory), in East-Central Europe (CE) and South-Eastern Europe (SE)

		CE				SE			
		Canopy		Understory		Canopy		Understory	
Variable set	Covariables	%	P	%	P	%	P	%	P
Stand (Sta)	None	8.0	**0.012**	10.0	**0.008**	33.0	**0.004**	25.1	**0.042**
Site (Sit)	None	-		5.0	0.084	17.0	**0.043**	28.0	**0.005**
Spatial (Spa)	None	10.0	**0.014**	15.0	**0.002**	49.0	**0.001**	34.0	**0.004**
Climate (Cli)	None	17.7	**0.011**	28.9	**0.001**	59.7	**0.001**	13.0	0.072
Sta	Sit + Spa + Cli	6.8	**0.026**	5.2	**0.035**	8.9	**0.024**	6.7	0.270
Sit	Sta + Spa + Cli	-		0.6	0.462	0.3	0.685	6.4	0.121
Spa	Sta + Sit + Cli	1.5	0.288	0.1	0.766	1.4	0.629	12.7	**0.033**
Cli	Sta + Sit + Spa	10.4	0.064	14.1	**0.013**	10.0	**0.053**	0.2	0.793
Sta + Spa	Sit + Cli	7.7	0.064	5.7	0.086	12.1	0.067	23.5	**0.044**
Sta + Sit	Spa + Cli	-		7.7	**0.038**	12.3	0.067	20.3	0.065
Spa + Cli	Sta + Sit	16.9	**0.021**	25.1	**0.002**	38.1	**0.003**	16.8	**0.048**
Sit + Cli	Sta + Spa	-		15.4	**0.016**	9.9	0.116	6.4	0.290
Sta + Cli	Spa + Sit	15.4	**0.034**	18.6	**0.006**	15.7	**0.034**	7.4	0.399
Spa + Sit	Sta + Cli	-		0.7	0.727	1.5	0.800	20.3	**0.030**
Sta + Sit + Spa	Cli	-		8.2	**0.073**	14.2	0.076	40.9	**0.013**
Spa + Sta + Cli	Sit	25.4	**0.005**	32.1	**0.001**	57.3	**0.001**	26.6	0.057
Spa + Sit + Cli	Sta	-		26.8	**0.002**	41.3	**0.003**	29.2	**0.022**
Sta + Sit + Cli	Spa	-		22.1	**0.005**	24.9	**0.011**	20.3	0.117
Sta + Sit + Spa + Cli	None	-		37.1	**0.001**	73.9	**0.001**	54.2	**0.007**

Note. The models includes all variables selected by forward selection in RDA separately in each variable set (grouping of variables), see Table 3. P = significance level (P < 0.05 in bold); % = ratio of data variability explained by the model.

ables in general. Climate operates at the largest intrinsic spatial scale and hence should have the highest impact, while stand and site variables vary at smaller scales and should have lesser effect on variation of mean BBN rating (Holdenrieder et al. 2004, Siefert et al. 2012). Large spatial extent of studies is important for understanding, predicting and managing diseases on a broader scale (Holdenrieder et al. 2004, Sturrock et al. 2011).

After partitioning of BBN severity variance, it was found that the larger proportion (more than half) of the explained variation was shared among variables in SE than in CE. This could suggest that BBN severity patterns are related to two or more intercorrelated sets of variables, the effects of which were not possible to disentangle, i.e. there is supposed collinearity among them. There were also found regional differences in the partitioning of the explained variance between canopy and understory trees. Except of SE understory trees, effect of climate remained highest also after partitioning of variance; more in SE than in CE in overall. The overlap between climate and/or another environmental variable with spatial variables may occur when some of environmental variables show trends across the study area. Such case was observed in our study, when annual precipitation was correlated to latitude (E) in CE (R = -0.29, P = 0.018, Fig. 3). Climate variables explained the largest part of the variability in mean BBN severity in SE, specifically for canopy trees (36.7%; Fig. 4C), while the spatial variables alone were most important for SE understory trees (12.7%, Fig. 4D). Large pure effects from individual sets of variables indicate that these may act as effective predictors for mean BBN severity at a given spatial scale. Strong climate effects can synchronize fluctuations of insect populations over large areas (Peltonen et al. 2002). Trees affected by inciting factors alone may recover quickly, but recovery is much slower if the trees are also affected by predisposing factors, such as climate (Sturrock et al. 2011). Thus, taking into account the positive association between the mean annual temperature (R = 0.48, P = 0.015; Fig. 3) or the temperature seasonality (R = 0.67, P < 0.001) and BBN severity rating of SE canopy trees observed in our study (Fig. 4C), the reinforcing effect of climate change on beech bark necrosis could be expected to be more serious mainly in beech forests of SE from lower altitudes than in other parts of the studied regions. Drought is generally considered as the most important limiting factor for beech under climate change scenarios (Geßler et al. 2007), and our results can be viewed as a support for assumed suppression of beech range within the southern Europe (see Kramer et al. 2010, Hanewinkel et al. 2012).

In CE, the correlation between BBN severity and the mean annual temperature was non-significant: with the annual precipitations, it was non-significant for the canopy trees and positive for the understory trees. Thus, we may suppose that an increased temperature and/or a reduced precipitation amount, associated with the climate change, should not negatively affect the beech susceptibility, and therefore the mean BBN severity in this geographic area.

Spatial structure in mean BBN severity was intercorrelated with environmental variables for whole stand, tree social status classes and canopy trees, but not for understory trees in SE (Fig. A2, 4; Table A3, 4). This pattern can suggest that locally specific processes affecting understory trees in SE, as pathogen dispersal and/or unmeasured environmental parameters that might vary spatially (Borcard et al. 1992, Wagner & Fortin 2005). Short-term and/or spatially limited factors causing acute stress (Allen et al. 2010, Sturrock et al. 2011), as extreme weather events, namely drought waves during the growth season and mild winters, are often observed and reported as factors inciting the incidence of complex "beech bark disease" in both Europe and North America (Houston et al. 1979, Chira & Chira 1997, 1998, Chira et al. 2003, Houston 2005). That was recently supported also by dendrochronological study of Kasson & Livingston (2012). On the other hand, excessive rainfalls and droughts trigger a necrotic disease caused by *Phytophthora* species. This disease may also be involved also in the complex of "beech bark disease" (Jung 2009). Unfortunately, we did not collect data on pathogens involved in BBN in single stands in our study; therefore it is possible that various biotic agents and different disease etiologies might be bulked together (cf. Jung 2009). This might also be reflected in lower amount of explained variability in mean BBN severity rating, particularly in CE.

Small effect of stand variables was statistically significant for canopy trees in both CE and SE, and for understory trees in CE, ranging from 5.2% to 8.9% (Table 4). Stand age was associated negatively with BBN in CE canopy trees (R = -0.29, P = 0.022), stocking positively in CE understory trees (R = 0.32, P = 0.011). Negative correlation was observed between stand structure (structure diversity) and BBN of SE canopy trees (R = -0.57, P = 0.003). Thus removal of understory trees, the social status class most affected by BBN severity, would not improve BBN infestation severity of canopy trees. From a silvicultural point of view, promotion of tree species diversity and adoption of multi-aged management systems (cf. Gamfeldt et al. 2013, O'Hara & Ramage 2013) from long-term perspective, and stand thinning (Bolte et al. 2009, Pichler et al. 2009) from short-term perspective might be the most viable strategies at regional level ensuring minimization of possible undesirable effects of predicted climate change on forests with higher incidence to beech bark necrosis. When spatial scale of observation or analysis changes, i.e. when the grain, spacing or extent is altered, statistical results are expected to change (Dungan et al. 2002, Gilbert & Bennett 2010). Population mean and variance, strength and character of spatial autocorrelation and multivariate relationships are the kinds of results that may change. Thus the remaining fraction of unexplained variation in mean BBN rating (26.1–74.6%) might represent not only random variability, but also variability related to measured or unmeasured variables which are not spatially autocorrelated on the scale used in this study (Borcard et al. 1992, Dungan et al. 2002, Wagner & Fortin 2005, Gilbert & Bennett 2010, Siefert et al. 2012). Those unmeasured variables may include for example susceptibility of individual trees to infestation linked to their genotype and phenotype (for "beech bark disease" see e.g. Gora et al. 1994, Krabel & Petercord 2000, Koch et al. 2010), variation of beech scale (*Cryptococcus* sp.) populations in their ability to infest host tree (Wainhouse & Howell 1983), damage to tree bark by wounds of artificial origin (Kunca & Leontovyč 1999, Kunca 2005) or induced by rodent injuries (Montecchio et al. 2011).

Conclusions

There were inter-regional differences in the amount of explained variability in mean BBN severity within the whole stand and tree social status classes, and in the sensitivity of canopy and understory trees to the environmental gradients investigated. The amount of explained variability was larger in SE (51.2–73.9%) compared to CE (28.4–37.1%); in CE, more variability was explained in canopy trees compared to understory trees, while the opposite was found in SE. Further, our analyses revealed that, at the scale used in our study, the climate was the strongest predictive environmental variable contributing to the mean BBN severity on landscape scale, more in SE than in CE. Considering the positive association between the mean annual temperature and the mean BBN severity in SE canopy trees, the discussed damage may be expected to be reinforced by negative impacts of climate change mainly in low situated beech forests of SE. In CE, the association between BBN severity and mean annual temperature was non-significant, while the annual precipitation was non-significant for canopy trees and positive for understory trees. We may assume that an increase of temperature or a shortening of the precipitation amount, associated with the expected climate change should not enhance the beech susceptibility to the damage in region of CE. For a better understanding of the relative importance of environmental and spatial variables on BBN severity, further research need to be performed on finer spatial scales (extent and grain), and also accounting for pathogens involved in the infestation.

Acknowledgements

The authors are grateful to anonymous referees for their valuable comments on previous version of manuscript, and to Dagmar Kúdelová and Peter Kaňuch for editing the English text. The study was supported from research projects funded by the Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic – VEGA No. 01/0362/13; 02/0027/13; 02/0055/10; and by the joint Project of the Institute of Forest Ecology of the Slovak Academy of Sciences, Zvolen (Slovakia) and the Forest Research Institute of the Bulgarian Academy of Sciences, Sofia (Bulgaria): The assessment of risk of the health status, structure and necrotisation in beech dendrocoenoses depending on changing anthropogenic conditions in Central and South-Eastern Europe.

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Appendix

Table A1 Descriptive statistics of the continuous variables used in the study for the studied regions (CE = Central-Eastern Europe, SE = South-Eastern Europe)

	Region	Mean	SD	Median	Min	Max	Lower quart.	Upper quart.
Explained variables Whole stand's characteristic								
S	CE	1.12	0.33	1.10	0.53	1.97	0.86	1.25
	SE	0.79	0.33	0.82	0.22	1.50	0.60	1.03
Canopy layer's characteristics								
C	CE	0.86	0.27	0.83	0.29	1.67	0.67	1.00
	SE	0.76	0.27	0.78	0.22	1.21	0.63	0.94
S-C	CE	1.29	0.42	1.17	0.63	2.59	1.00	1.61
	SE	1.14	0.71	1.00	0.18	3.00	0.71	1.44
U	CE	1.68	0.57	1.68	0.50	3.00	1.20	2.00
	SE	1.29	1.11	1.00	0.00	4.00	0.75	1.40
Explanatory variables Stand charact								
abun	CE	80.8	22.4	91.0	25.0	100.0	60.0	100.0
	SE	96.5	8.4	100.0	50.0	100.0	98.0	100.0
age*	CE	98.0	43	90	40	250	70	103
	SE	83.0	20	80	50	135	70	90
struct	CE	18.3	10.2	19.0	0.0	39.0	12.0	26.0
	SE	4.0	5.3	2.3	0.0	22.0	0.0	6.0
stock*	CE	0.71	0.11	0.70	0.40	1.00	0.60	0.80
	SE	0.67	0.10	0.70	0.40	0.80	0.60	0.70
Site char								
PSR	CE	1,004,342	173,462	1,026053	513,400	1,329,043	908,915	1,127,760
	SE	1,121,300	177,115	1,079301	784,908	1,485,937	982,031	1,265,911
Slope*	CE	20.8	9.6	20.8	4.8	41.4	13.5	26.4
	SE	18.0	7.6	17.1	4.1	35.7	13.5	23.4
curv*	CE	0.171	2.123	0.000	-6.683	5.992	-0.807	1.152
	SE	-0.028	1.301	-0.196	-3.233	4.016	-0.784	0.686
Explanatory variables Spatial charact.								
N	CE	48.7164	0.5058	48.7158	47.2575	49.6196	48.5587	48.9959
	SE	42.6067	0.5205	42.7294	41.8777	43.950	42.0784	42.884
E	CE	20.1711	1.8500	19.8000	17.0817	25.6738	18.9707	21.2511
	SE	24.3590	1.4162	24.1593	21.6833	27.633	23.3492	24.660
Bioclim. charact.								
alt	CE	717	224	685	300	1250	545	890
	SE	934	330	975	300	1550	700	1150
MAT	CE	6.2	1.3	6.2	3.5	9.3	5.3	7.0
	SE	8.0	1.8	7.9	4.4	12.3	7.0	9.2

Table A1 (continuation)

	region	mean	SD	median	min	max	Lower quart.	Upper quart.
TS	CE	736.0	26.6	737.0	683.0	787.6	715.9	755.2
	SE	713.1	33.0	705.7	649.9	793.1	691.7	737.9
MTCM	CE	-8.5	1.1	-8.6	-10.0	-4.8	-9.3	-8.0
	SE	-5.9	1.5	-6.1	-8.4	-0.9	-6.6	-5.4
MTDQ	CE	-2.4	1.3	-2.7	-4.7	0.6	-3.4	-1.6
	SE	7.4	7.2	10.4	-2.7	20.7	0.1	13.2
AP	CE	817	119	810	573	1137	710	884
	SE	660	53	645	568	777	627	695
PS	CE	33.6	5.7	33.0	24.0	49.0	30.0	37.0
	SE	23.0	2.4	22.0	18.0	27.0	21.0	25.0
PDQ*	CE	134	25	136	90	192	115	151
	SE	128	14	125	102	153	119	140

Note. Abbreviations and units: see Table 2. See Material and Methods for detailed description of variables. *All variables besides C, S-C, age, stocking, slope, curvature, and PDQ are significantly different between regions at $P < 0.05$ (Mann-Whitney U test, *n*: CE - 68, SE - 46 stands).

Table A2 Variance in mean beech bark necrosis severity for whole stand (Stand) and tree social status classes (Tree social classes) explained by stand, site, spatial, and climatic variables retained after forward selection in RDA based on each set of variables (i.e. separately in each set), in East-Central Europe (CE) and South-Eastern Europe (SE)

	Variable set	Stand				Tree social classes		
		variable	%	*P*		variable	%	*P*
CE	Stand	age	6.0	0.042	Stand	age	8	0.012
	Site	-	-	-	Site	curv	5	0.080
	Spatial	NNEE	9.0	0.020	Spatial	NNE	10	0.010
	climate	PDQ	11.0	0.007	climate	TS	10	0.012
		MTDQ	6.0	0.033		MTCM	3	0.082
		alt	5.0	0.048		PREC	6	0.044
		Model	22.3	0.001		Model	19.2	0.003
		Total	29.1	0.001		Total	28.4	0.001
SE	Stand	-	-	-	Stand	struct	17	0.018
	Site	-	-	-	Site	rad	16	0.023
	Spatial	N	37	0.001	Spatial	NNNE	31	0.001
		NNN	9	0.005		EEE	11	0.017
		Model	46.4	0.001		N	6	0.100
						Model	47.5	0.001

Note. For variables' description see Table 2. Total - variance explained by all variables selected by forward selection in RDA. *P* - significance level; % - ratio of data variability explained by the model.

Table A2 (continuation)

Variable set	Stand				Tree social classes		
	variable	%	*P*		variable	%	*P*
climate	MTDQ	41	0.001	climate	MTDQ	31	0.001
					TS	9	0.040
					Model	40	0.001
	Total	51.2	0.001		Total	60.3	0.001

Table A3 Significance of RDA models and variation partitioning among stand, site, spatial and climatic variables explaining beech bark necrosis severity for whole stand (Stand) and tree social status classes (Tree social classes), in East-Central Europe (CE) and South-Eastern Europe (SE)

		Stand				Tree social classes			
		CE		SE		CE		SE	
Variable set	Covariables	%	*P*	%	*P*	%	*P*	%	*P*
Stand (Sta)	None	6.0	**0.042**	-		8.0	**0.012**	17.0	**0.018**
Site (Sit)	None	-		-		5.0	0.080	16.0	**0.023**
Spatial (Spa)	None	9.0	**0.020**	46.4	**0.001**	10.0	**0.010**	47.5	**0.001**
Climatic (Cli)	None	22.3	**0.001**	41	**0.001**	19.2	**0.003**	40.0	**0.001**
Sta	Sit + Spa + Cli	6.6	**0.017**	-		5.7	**0.025**	3.4	0.234
Sit	Sta + Spa + Cli	-		-		1.1	0.383	3.5	0.221
Spa	Sta + Sit + Cli	0.8	0.391	9.7	**0.022**	1.0	0.426	9.6	0.246
Cli	Sta + Sit + Spa	16.7	**0.005**	4.9	**0.044**	10.8	**0.031**	2.9	0.668
Sta + Spa	Sit + Cli	6.8	0.056	-		6.4	0.069	13.8	0.188
Sta + Sit	Spa + Cli	-		-		8.5	**0.025**	9.6	0.097
Spa + Cli	Sta + Sit	23.1	**0.001**	51.2	**0.001**	17.5	**0.006**	37.3	**0.005**
Sit + Cli	Sta + Spa	-		-		13	**0.030**	6.8	0.461
Sta + Cli	Spa + Sit	20.0	**0.004**	-		14.5	**0.016**	6.0	0.546
Spa + Sit	Sta + Cli	-		-		2.3	0.446	13.7	0.193
Sta + Sit + Spa	Cli	-		-		9.2	0.052	20.2	0.103
Spa + Sta + Cli	Sit	29.1	**0.001**	-		23.6	**0.002**	44.6	**0.005**
Spa + Sit + Cli	Sta	-		-		20	**0.007**	43.5	**0.004**
Sta + Sit + Cli	Spa	-		-		18.2	**0.009**	12.7	0.233
Sta + Sit + Spa + Cli	None	=		=		28.4	**0.001**	60.3	**0.001**

Note. The models includes all variables selected y forward selection separately in each variable set (grouping of variables), see Table 3. *P* - significance level ($P < 0.05$ in bold); % - ratio of data variability explained by the model.

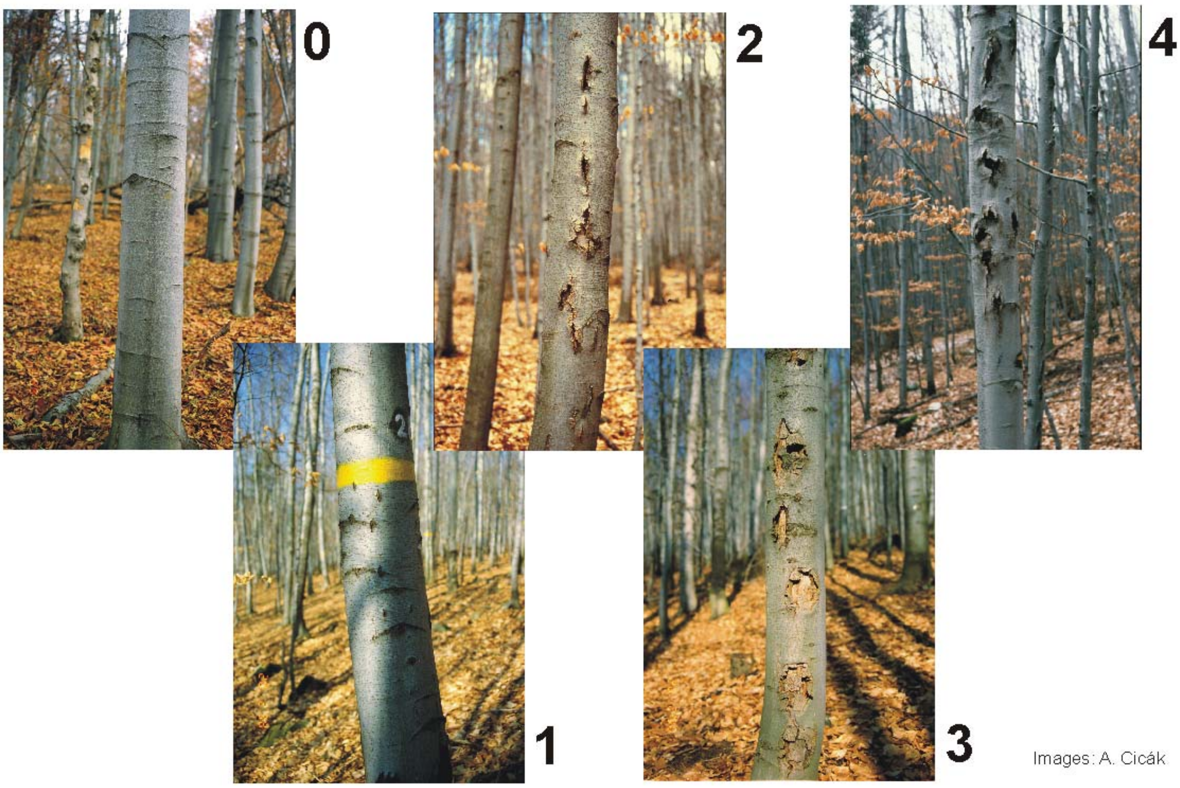

Figure A1 Stems of European beech ranked with ordinal scale ratings for bark necrosis severity. See Table 1 for description of particular ratings.

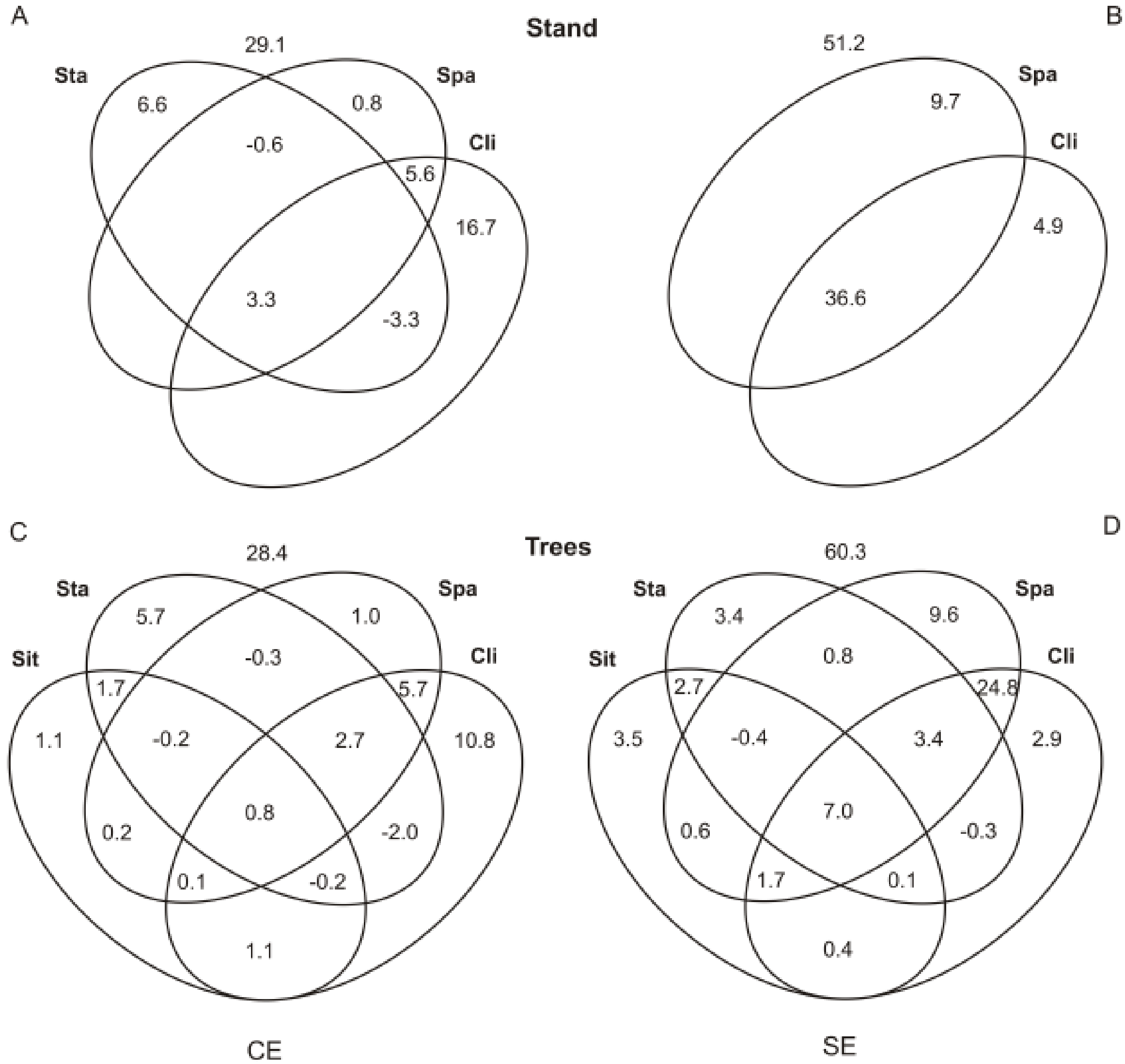

Figure A2 Variation partitioning between stand (Sta), site (Sit), spatial (Spa) and climate (Cli) variables for mean beech bark necrosis severity of stand (A, B) and three tree social status classes (i.e., canopy, sub-canopy and understory trees; C, D) in East-Central Europe (CE; A, C) and South-Eastern Europe (SE; B, D). Only variables selected by forward selection in RDA analyses (Table A2) were used for variance partitioning. The total variance explained by all variables is above the Venn diagram. For significance see Table A3.