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Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study

Andreas Bolte · Lutz Hilbrig · Britt Maria Grundmann ·
Andreas Roloff

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Abstract

• **Context** It is assumed that climate change will favour European beech (*Fagus sylvatica* L.) to Norway spruce (*Picea abies* [L.] Karst.) at its northern range margins due to climate change and induced disturbance events.
• **Aims** An old-growth mixed forest of spruce and beech, situated near the northern beech margin, was studied to reveal effects of disturbances and response processes on natural forest dynamics, focussing on the understory.
• **Methods** We carried out analyses on understory dynamics of beech and spruce in relation to overstory release. This

was done based on a sequence of stand and tree vitality inventories after a series of abiotic and biotic disturbances.

• **Results** It became apparent that beech (understory) has a larger adaptive capacity to disturbance impacts and overstory release (68 % standing volume loss) than spruce. Understory dynamics can play a key role for forest succession from spruce to beech-dominated forests. Disturbances display an acceleration effect on forest succession in the face of climate change.

• **Conclusion** Beech is poised strategically to replace spruce as the dominant tree species at the study area. Due to an increasing productivity and a lower risk of stand failure, beech may raise into the focus of forestry in southern Sweden.

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A. Bolte (✉) · L. Hilbrig
Johann Heinrich von Thünen-Institute (TI), Institute of Forest
Ecosystems, A.-Möller-Straße 1,
16225 Eberswalde, Germany
e-mail: andreas.bolte@ti.bund.de

L. Hilbrig
e-mail: lutz.hilbrig@ti.bund.de

A. Bolte
Department of Silviculture and Forest Ecology of the Temperate
Zones, Georg-August-University Göttingen, Büsgenweg 1,
37077 Göttingen, Germany
e-mail: abolte@gwdg.de

B. M. Grundmann · A. Roloff
Institute of Forest Botany and Forest Zoology, Technical
University of Dresden (TUD), Piennner Straße 7,
01737 Tharandt, Germany

B. M. Grundmann
e-mail: grund@forst.tu-dresden.de

A. Roloff
e-mail: rolloff@forst.tu-dresden.de

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1 Introduction

Over the past 100 years, mean annual air temperature in Sweden has increased to about 1 °C (Christensen et al. 2007). For southern Sweden, air temperature projections point to a warming by a further 4 °C and mean precipitation increase by 11 % until the year 2100, triggered by anthropogenic climate change (Lind and Kjellström 2008). The warming tendency may result in an extended growing season (Christensen and Christensen 2007). These long-term effects may be overruled by frequent and intensive weather extremes like heat waves and drought episodes as well as intense precipitation events and storms (Nikulin et al. 2011; Donat et al. 2011). For the forests in the region, those increasing abiotic impacts and accompanied biotic threats

like bark beetle gradations (Schlyter et al. 2006; Jönsson et al. 2007, 2009) form a specific disturbance regime.

The recent natural vegetation in the boreo-nemoral zone (sensu Sjörs 1999) of Southern Scandinavia constitutes of mixed spruce–beech forests. It is there that the northern margin of beech range is overlapping the southern margin of spruce in the lowlands (Björkman 1999).

The long-term warming is reputed to increase the competitive ability of ‘nemoral’ beech compared to the currently dominant ‘boreal’ spruce (Grundmann et al. 2011). It is believed that spruce is more susceptible to heat waves and drought due to its shallow root systems (e.g. Schmid 2002) and its adaptation to cold and humid environments, particularly to the northern spruce races (Latałowa and van der Knaap 2006).

Previous analyses in the old-growth spruce–beech forest at Siggaboda reserve (Småland, Southern Sweden) addressed stand dynamics and overstory growth performance (Bolte et al. 2010, Grundmann et al. 2011). This included distinct storm, drought and biotic disturbance impacts on forest structure from 2004 to 2007 and long-term changes in the competing interaction between spruce and beech during the past decades before the disturbances occurred. This study, in contrast, focusses on understory growth dynamics and on its role for post-disturbance forest succession in this natural forest. Moreover, we extended the disturbance analyses with additional interim assessments on the tree health status in 2009 and have performed a new stand growth analysis due to the first re-inventory of the stand in 2011. With this information, we want to answer the questions on (1) how (differently) beech and spruce understory are responding to climate change-induced disturbances and overstory release, (2) what role understory dynamics play in natural forest dynamics, and (3) how on-going disturbance affects the over- and understory interaction, regarding a reputed forest succession from spruce- to beech-dominated forest vegetation.

2 Materials and methods

2.1 Site types

From 2004 to 2011, a long-term study on stand dynamics was conducted at the Siggaboda forest nature reserve in Southern Sweden (56°27' N, 14°33' E, see also Bolte et al. 2010). The reserve of 70 ha lies near the border between Småland and Blekinge provinces at the southern edge of the boreo-nemoral zone (Sjörs 1999). The climate is humid with a mean annual temperature of 6 °C and an annual precipitation of around 700 mm year⁻¹. Mean monthly temperature ranges from −3 °C in January to 15 °C in July (Raab and Vedin 1995).

The bedrock is granite gneiss, and massive boulders of up to 5 m in height are very abundant in the central old-growth

area of 5 ha where the mixed spruce–beech stand is located. The fine textured soil material originating from bedrock and admixed moraine sediments is silt- and sand-dominated with low clay content. The relatively poor nutrient content of the parent soil material and the humid climate have induced the development of Haplic Podzols (FAO 2006), overlain by raw humus (C/N ratio, 27 to 31; pH (KCl), organic layer 3.0 to 3.6, mineral soil 3.4 to 3.9 Bolte et al. 2010).

The main feature of the nature reserve is a central 5 ha old-growth mixed forest of spruce and beech. The beech individuals are up to 250 years old, whereas the spruce individuals reach a maximum age of 140 to 150 years (Grundmann et al. 2011). It is protected since the 1940s, and in 1995, a 65-ha buffer zone was created, featuring coniferous stands of spruce and Scots pine (*Pinus sylvestris* L.), now between 80 and 115 years old. According to a detailed map of Siggaboda reserve from 1909 by the county authorities (Hannon et al. 2010), the core area seems to have been nearly untouched by logging for at least 100 years, since the then mapped 150-year-old *Picea–Fagus* stand still exists. However, some extensive use of the forest cannot be excluded (Björkman and Bradshaw 1996).

At the beginning of the study in December 2004, spruce trees were the most abundant tree species followed by beech (Bolte et al. 2010). The stand was then subjected to a succession of intensive disturbance events starting with a hurricane ‘Gudrun’ in January 2005 featuring wind speeds over 30 m s⁻¹ (108 km h⁻¹) over large areas of Southern Sweden (Røsting and Kristjánsson 2008) and leading to large windthrown forest areas in the region. The growing season of the subsequent year, 2006, was extraordinary hot, and there was a mid-summer heat and drought period in June and July (precipitation, 28 and 58 mm; temperature, 1.4 °C to 4.5 °C above means; Bolte et al. 2010), which lasted well into the autumn with mean temperatures in October over 10 °C (WeatherOnline 2011). In 2007, the first indications of a spruce decline due to a bark beetle (*Ips typographus*) outbreak were visible. This decline process has continued until the last stand recording in April 2011 (Table 1).

2.2 Field assessments

For stand assessments, we applied the ‘core plot’ approach adopted from the forest nature reserve monitoring in Northern Germany (Meyer 2005). Following this, a 1-ha square core plot was placed subjectively in the centre of the reserve's old-growth area in order to select a typical structure of the least disturbed old-growth forest. We divided the plot into 25 subplots of 400 m² with a grid of 20 m (Meyer et al. 2001). The 36 edge points of the subplots were permanently marked with wooden stakes, and we determined their positions using an ultrasonic hypsometer

Table 1 Stand structural traits of the core plot stand (1 ha) including standing and living trees; dbh is the diameter at breast height (1.3 m above ground); data includes tree increment and tree ingrowth

	Species	Mean dbh dg (cm)	Mean height hg (m)	Tree number (n·ha ⁻¹)	Basal area (m ² ·ha ⁻¹)	Growing stock (m ³ ·ha ⁻¹)
Slight variation compared to values reported for 2004 in Bolte et al. (2010) are due to reassessments of tree status (lying/standing, living/dead) in 2004 by 2011 status	December 2004					
	Norway spruce	35.9	28.0	264	26.7	350.2
	European beech	19.9	16.4	182	5.5	45.2
	Other species	20.8	16.1	40	0.8	6.7
	Total			486	33.0	402.1
	April 2011					
	Norway spruce	24.0	21.9	151	6.7	78.9
	European beech	19.9	15.9	181	5.6	46.3
	Other species	14.5	16.2	31	0.5	4.4
	Total			363	12.9	129.6

(Vertex III, Haglöf Inc. Sweden) and a compass (PM-5/400PC, Suunto Inc., Finland).

Both in December 2004 and April 2011, all trees and snags with a diameter at breast height (*dbh*) of 7 cm and larger were recorded on the entire core plot. In 2004, each selected tree specimen was temporarily marked and numbered with a tagging system (Signumat, Latschenbacher, Austria). The recordings included stem position using hypsometer and compass, tree species and diameter at breast height (*dbh*) using girth tape. In a central subsample of nine subplots (0.36 ha area), we additionally recorded tree crown base height (*cbh*), crown mid height (*cmh*, where maximum crown width occurs) and tree top height (*th*). Before the start of the growing season in 2005, we made a single recording of the horizontal crown extension from the orthogonal projection of eight outermost crown edge points. The positions of the edge points were determined and marked using a 45° mirror with sighting aperture and position marking system (Göttingen University, Germany). Subsequently, we leveled it with their cardinal coordinates with the above-mentioned equipment. In July 2007 and June 2009, the vitality status of all trees within the core plot was assessed by identifying dead and dying trees and the causes for decreased vitality.

2.3 Data analysis

We used the software bundle Statistica 9 (StatSoft 2009) for all statistical analyses.

Analyses on stand structure dynamics from 2004 to 2011, including assessments on crown dimension (*cd*), basal area (*ba*) and wood volume (*wv*), as well as three-dimensional stand mapping were performed with the stand simulator BWIN-Pro 7 (Nagel et al. 2006). Recorded tree dimension increments (*cd*, *ba*, *wv*) from 2004 to 2011 were linearly interpolated to obtain values for the intermediate vitality assessment dates in 2007 and 2009. In 2011, sapling ingrowth was also recorded.

Non-measured height values of the outer subplots were derived from the measured diameter at breast height (*dbh*) with a stand height curve based on the Petterson function (Petterson 1955). Missing crown dimension data derived from measured *dbh* and derived height data applying an empirical function of Pretzsch et al. (2002).

The competition–growth relationships within the study period from 2004 to 2011 were analysed calculating a competition index *CI* (Pretzsch et al. 2002) for each tree specimen of the core area defined as reference tree. *CI* is a distance- and dimension-dependent competition index that considers differences of height and crown extension between reference tree and competitors. We identified the competitors of the reference tree applying the ‘virtual reverse cone’ method with 60° vertex angles of the cone and a cone basis height of 60 % of tree height. All surrounding tree specimens with tree tops within the virtual cone were defined as competitors of the reference tree. More detailed information on the procedures is provided by Bolte et al. (2010).

Based on the repeated stand inventory in 2011, we also calculated the growth response of spruce and beech to the disturbance event sequence. We used relative increment parameters like *dbh* and tree height increment from 2004 to 2011 in relation to the initial dimension in 2004. This was done in order to compare species-specific asymmetry of dimension increment (cf. Yue et al. 2008) along the size spectrum of both species. This allows the comparison of tree cohorts differing in age which are often found for understory beech in the core plot stand.

3 Results

3.1 Disturbance impacts and overstory release

Total growing stock of the old-growth stand in the core plot increased from 539 m³ ha⁻¹ in 2004 to 565 m³ ha⁻¹ in 2011 (Fig. 1). However, the share between living stand and dead

Fig. 1 Total stock dynamics from December 2004 to April 2011 including living as well as standing and lying dead stand volume. 'Old' lying dead wood volume found at the study commencement in December 2004 is not included

wood components changed drastically due to disturbance events from 25.5 % dead wood proportion in 2004 to 77.1 % in 2011. The different disturbance events from 2005 to 2007 (storm, drought and starting bark beetle attacks) and their impacts on living (overstory) stand structure were already presented by (Bolte et al. 2010). The extended time series with the inventories in 2009 and 2011 showed a continued and increased biotic disturbance impact through spruce bark beetle infestations (*I. typographus* L.). Regarding growing stock dynamics of both living and dead wood stand compartments (Fig. 1), we found in April 2011 only 32 % of the living standing wood volume compared to December 2004 (402.1 m³), whereas this value was almost 60 % in June 2007 and almost 90 % in May 2005 after the 'Gudrun' storm (Fig. 1, Bolte et al. 2010). These changes were almost completely due to a decline of dominating overstory spruce in the stand losing 79 % of living wood volume; beech and other rare tree species remained nearly unaffected.

Among dead wood volume, a strong variation of standing and lying dead wood compartments is visible (Fig. 1). The

increase of lying dead wood material after the storm from 2004 to 2005 was overruled by the raise of standing dead wood volume in the following years with bark beetle damages. However, a huge number of standing dead trees were wind-broken from 2009 onwards, leading to a high lying dead wood volume of 260 m³ in 2011, 93 % of which were Norway spruce. A dense dead wood coverage was found in 2011 in several parts of the core plot where often two or more stems were lying upon each other. European beech was nearly unaffected by the disturbance sequence.

The three-dimensional view onto the core plot stand dynamics (Fig. 2) illustrates the drastic changes in the mixed stand structure and the overstory release. As the result of disturbance event sequence, living spruce was nearly absent in 2011 in the southern part of the core plot where the trees grow on a slightly elevated boulder ridge. Several spruce trees of medium to low dimension were still found in a central depression within the core plot and in the northern part of the plot. Relative to spruce, beech trees were much more abundant and the dominating structural element in 2011.

Fig. 2 Core plot living stand dynamics from 2004 (left figure) to 2011 (right figure). Stand visualization with BWIN-Pro 7 (standing and lying dead trees are not shown), tree dimension changes and tree ingrowth are included. Cone-shaped crowns: Norway spruce, elliptical crown shape: European beech and other broadleaved tree species (very few trees)

3.2 Understory response

Relative dimension increment of trees during and after the disturbance succession increased with decreasing tree size (Fig. 3). This asymmetric growth was found for both species regarding the relative increment of *dbh* (*idr*) and top height (*idh*) of trees measured both in 2004 and 2011. Thus, understory trees ($dbh < 20$ cm, $h \approx 15$ m to 17 m, cf. Peterson curve in Bolte et al. 2010) responded much stronger in growth to the disturbance impacts than the overstory trees. However, more remarkable is that this asymmetry was significantly higher for beech than for spruce (ANCOVA, Table 2) leading to a considerably higher relative diameter and height increment of understory beech compared to that of spruce. The decrease of tree competition during the study period correlates with relative tree volume increment from 2004 to 2011 (Fig. 4). Though the lowering of tree competition index (*CI*) was strongest for several specimens of the spruce collective, the growth-stimulating effects of competition decrease were considerably higher for beech after reaching a threshold of about 1 *CI* unit. The increment superiority of beech decreased with increasing *CI* when compared with spruce. An analysis of covariance (ANCOVA) results in a significant tree species effect on competition–volume increment relations (Table 3). Results of both analyses demonstrate a high growth potential of beech understory during and after the disturbance processes in the old-growth part of the stand. The considerably higher performance of beech understory compared to that of spruce indicates that beech has a competitive advantage compared to spruce in recovery after disturbance.

4 Discussion

4.1 Disturbances and overstory dynamics

The total effect of disturbance on the overstory at the reserve's core plot during the study period represents a succession of individual impacts due to warming, storm, drought and bark beetle effects; the latter reputed to be

increasingly relevant for future dynamics in southern Scandinavia due to climate change (Schlyter et al. 2006; Christensen and Christensen 2007; Jönsson et al. 2007, 2009; Blennow and Olofsson 2008). The remarkable mechanical resistance of the stand to the disastrous storm ‘Gudrun’ in Januar 2005 (75 million m³ loss of standing wood volume, Komonen et al. 2011) was extensively discussed by Bolte et al. (2010). The following loss of 2/3 of the living standing wood volume until 2011 after the storm and drought events triggered by bark beetle infestations are in line with studies and observations in other spruce dominated forests in Europe. Similar spruce outbreak dynamics were reported after large storm events and droughts like Lothar 1999 and the 2003 drought in Switzerland (Gugerli et al. 2008), several storms in the 1980s and subsequent drought years in the 1990s in the Bavarian Forest (Müller et al. 2008) or the 2003 drought event in the Polish Beskid mountains (Grodzki 2010). Our found bark beetle disturbance dynamics and its triggering process are very similar to those found at Osby nature reserve about only 50 km southeast of Siggaboda (Komonen et al. 2011), with one exception. In this pure spruce stand, spruce bark beetle killed all spruce specimens in 2006. As beech is reputed to mitigate the risk of bark beetle attacks (Pretzsch and Schütze 2005; Seidl et al. 2008), the prolonged decline of spruce at Siggaboda old-growth area may be due to the mixed forest conditions there.

4.2 The role of understory dynamics for forest succession

The found strong growth response of beech understory to overstory release or liberation is remarkable, and at the first glance, this contradicts ideas of this species as a slow-growing late-successional tree species (Ellenberg 1988). However, at Siggaboda nature reserve, beech is growing not too far from its northern distribution margin in Sweden (Mattarp, northern Småland, Björkman 1996; Kyrkerud, southern Värmland, Fang and Lechowicz 2006). The short growing seasons and low winter temperatures (Bolte et al. 2007) strongly limited growth conditions, which clearly favours spruce to beech at the time the study was initiated

Fig. 3 Relationships between (a) breast height diameter (*dbh*) and relative diameter increment (*idr*) for beech and spruce; (b) tree top height (*th*) and relative height increment (*idh*); only tree specimen measured twice in 2004 and 2011 with positive increment are included. Tree species effects on the linear relationships are significant according to an analysis of covariance (ANCOVA, see Table 2)

Table 2 Analysis of covariance (ANCOVA), univariate test results of tree species effects on relationships between relative increment (*idr*, *ih*) and tree dimension (*dbh*, type III decomposition models with highest coefficients of determination)

	SS	DF	MS	F	P
<i>idr</i> ($r^2=0.33$)					
<i>dbh</i>	3,209.56	1	3,209.56	46.8913	<0.01
Tree species	20,521.32	2	10,260.66	149.9071	<0.01
Error	7,529.15	110	68.45		
Total	38,453.11	113			
<i>ih</i> ($r^2=0.66$)					
<i>th</i>	4,432.99	1	4,432.99	20.07841	<0.01
Tree species	23,436.64	2	11,718.32	53.07594	<0.01
Error	18,766.64	85	220.78		
Total	5,5672.72	88			

dbh breast height diameter (1.3 m tree height) (cm), *idr* relative *dbh* increment 2004–2011 (%), *th* tree top height (m), *ih* relative height increment 2004–2011 (%); only twice in 2004 and 2011 measured spruce and beech specimens with positive increment were included in the analyses

in 2004 (Bolte et al. 2010). Comparative growth studies on old specimens of both species revealed that beech has already picked up in radial increment relative to spruce over the last decades. This was interpreted as a climate change assisted improvement of beech growth compared with spruce (Grundmann et al. 2011). Beech understory is in particular favoured by the decrease of vertical competition pressure of the spruce dominated canopy, and it is obviously

Table 3 Analysis of covariance (ANCOVA), univariate test results of tree species effects on relationships between relative increment (*ivr*) and tree competition status (type III decomposition models with highest coefficients of determination)

	SS	DF	MS	F	P
$\ln [ivr]$ ($r^2=0.38$)					
$\ln [-iCI]$	2.1931	1	2.19306	28.937	<0.01
Tree species	178.9821	2	89.49104	1180.837	<0.01
Error	5.2292	69	0.07579		
Total	209.2788	72			

ivr relative stem volume increment 2004–2011 (%), $-iCI$ decrease of competition index (CI, no unit) from 2004 to 2011

Only twice in 2004 and 2011 measured spruce and beech specimens with positive volume increment (derived from height and diameter increment) were included in the analyses

more successful than spruce understory in exploiting increased supply of growth resources such as light, water and nutrients. This asymmetric competition favouring beech “from below” is in line with observations and analyses in several strict forest nature reserves in Germany where beech is increasingly dominant in mixed stands previously dominated by other species (Meyer 2005). High morphological plasticity of beech and low light demand (Emborg 1998; Löff et al. 2005; Schröter et al. 2012) are important traits for growing under high interspecific competitive pressure of dominating spruce. Under these conditions, it is very likely that several trees of the beech understory are much older than those of spruce with comparable size, persisting sometimes for several decades with low performance. Ammer et al. (2008) reported on ontogenetic effects on beech seedling development under spruce canopy. Under identical light regimes, older seedlings exhibited a higher height growth than younger ones. Compared to spruce, beech is superior in area acquisition applying a particular ability of lateral and vertical expansion, encircling competitors and filling gaps after disturbances (Pretzsch and Schütze 2005). With this adaptation to disturbance-induced overstory release, beech understory can play a key role for forest succession from spruce to beech-dominated forests at Siggaboda area and probably beyond that. Due to this, single disturbances or disturbance sequences may have an ‘accelerating function’ for forest dynamics (cf. Fischer et al. 2002) and for forest succession on stand scale in the face of climate change (Mailly et al. 2000).

Fig. 4 Relationships between decrease of competition index ($-iCI$, log transformation) from 2004 to 2011 and relative volume increment (*ivr*, log transformation) for beech and spruce; only tree specimen measured twice in 2004 and 2011 with positive increment of both diameter (*id*) and height (*ih*) are included. Tree species effects on the linear relationships are significant according to an analysis of covariance (ANCOVA, see Table 3)

4.3 Theory for climate change-induced forest succession

Previous and current presented analyses of stand structure dynamics are summarized within a conceptual scheme for climate change-induced forest succession in the Siggaboda area (Fig. 5). The ‘impact and response pathways’ are divided

Fig. 5 Conceptual scheme for climate change-driven forest succession at Siggaboda core plot area: interacting disturbance and resilience processes of stand dynamics induced by warming, storm, drought, and bark beetle effects (framed). Major processes are indicated with *solid arrows*; associated processes with *dashed arrows*

into warming, storm and drought effects of climate change. Direct storm impacts include the accumulation of windthrown and damaged spruce wood volume that represented a surplus of breeding material for bark beetles, in particular *I. typographus* L (Schelhaas et al. 2003; Økland and Berryman 2004). Though only low volumes of wind-damaged spruce trees were found within the 5-ha-old growth area, much higher volumes were found in the surrounding buffer zones with pure coniferous stands where the damaged and dead spruce wood material was left to promote biodiversity of xylobiontic fauna (cf. Komonen et al. 2011). The surplus of breeding material decreased the intensive intraspecific competition among the spruce bark beetles that limits their reproductive success and thus keeps their population on an endemic level (Eriksson 2007). Here, an interaction with warming effects occur: the warm and exceptionally long lasting growing season in 2006 as well as the warm winter 2006/07 and early spring 2007 (Bolte et al. 2010) provided good swarming, reproduction and hibernation conditions that should enable two bark beetle generations to complete their development (Komonen et al. 2011). Moreover, the second generation sustained during winter (cf. Jönsson and Bärning 2010). It is likely that first bark beetle attacks on standing living spruces occurred in 2006, the second summer after the storm (cf. Schroeder 2001) when their defensive system were weak during the summer drought. In particular, the highest and oldest spruce specimens seemed to be among the first trees that were attacked due to a high drought stress disposition and a low defensive system status (Fig. 3, Bolte et al. 2010). This disposition is due to storm-induced tree movement of larger spruce trees and lifting of the soil-root plate may have led to hidden but extensive breakage of the finer roots (Coutts 1983, 1986) which have an important

function in water and nutrient acquisition (cf. Atkinson 2000). Thus, the 2006 drought resulted in a sensitive collective of spruce trees, which, more than likely have partly damaged and shallow root systems (Puhe 2003) causing a problem for large, tall trees (around 40 m) with high transpiration (Herzog et al. 1998) and increasing xylem pressure of crown branches for water transport against gravity (cf. Koch et al. 2004). Beside probable vitality and productivity losses, the low water status of spruce decreases its major defensive ability against bark beetles based mainly on resin exudation (Franceschi et al. 2005).

Despite the probable initial bark beetle attacks on weakened living spruce during the drought summer of 2006, a prolonged mortality period from 2007 to 2011 (cf. Faccoli 2009) occurred that left only a few spruce trees alive. This is due to the increasing bark beetle population growth. With raising breeding material provision, bark beetles can overcome the defence system of less weakened spruce, leading to this spruce overstory decline.

This overstory spruce decline is accompanied with the previously discussed performance and growth stimulation of the beech understory outcompeting spruce understory. This results in beech becoming the dominant tree species in the overstory as well as the understory, climate change-induced disturbances have accelerated this process.

5 Conclusions

With its remarkable adaptive capacity to regional climate change including both long-term warming and disturbance events, beech is poised strategically to replace spruce as the

dominant structural element at Siggaboda old-growth area. In accordance with other consistent analyses about disturbance impacts on spruce in Sweden (Schlyter et al. 2006; Jönsson et al. 2007, 2009; Komonen et al. 2011), the outcome of this study suggests that disturbance impacts as well as overstory release can restrict the spruce's competitive ability to beech in Southern Scandinavia. The risk of a catastrophic loss of high timber volumes in spruce stands will probably increase as well as the efforts to maintain forest structures against an increasing successional pressure (cf. Bolte et al. 2009). Moreover, more frequent storm impacts will lead to a pervasive and significant growth reduction of spruce on a landscape scale that was found for years after the 'Gudrun' storm (Seidl and Blennow 2012). Thus, beech and perhaps also other broadleaved species may rise into the focus of forestry in southern Sweden due to higher productivity and lower risk of stand failure.

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