



# Restrictions on natural regeneration of storm-felled spruce sites by silver birch (*Betula pendula* Roth) through limitations in fructification and seed dispersal

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## Abstract

Particularly after disturbance events, the early successional colonist *Betula pendula* Roth is experiencing renewed silvicultural interest with respect to the natural regeneration of large disturbed forest areas. In a case study, we therefore studied the seed dispersal of *B. pendula* from two adjacent spruce stands to large storm-felled sites at high altitudes in the Thuringian Forest (Germany) over a 2-year period. We applied inverse modelling to describe the distance-dependent seed distribution using a negative exponential kernel and seed production function of birch seed trees. Maximum seed numbers of 2015 n m<sup>-2</sup> (non-mast year) and 9557 n m<sup>-2</sup> (medium year) occurred within 40–50 m distance to a seed tree. The predicted seed production rate of a birch seed tree with a reference dbh of 20 cm was approximately 350,000 n tree<sup>-1</sup> (non-mast year) and 1,500,000 n tree<sup>-1</sup> (medium year). Regardless of the seed crop, the dispersal distances were similar in both years. The isotropic model showed mean dispersal distances of 86 and 97 m (uphill) and 367 and 380 m (downhill) for the 2 years of seed sampling. No directionality in seed dispersal was found. The findings showed birch seed dispersal to be strongly influenced by site inclination, seed tree position (valley, slope or plateau) and distance to the storm-felled site. Furthermore, the seed shadow is influenced by the number of seed sources. Therefore, risk-adapted forest management should include the ‘spatial optimization’ of birch seed trees, ideally creating a network of small seed tree groups scattered more or less regularly within pure conifer forests.

**Keywords** Silver birch · Seed rain · Pioneer trees · Disturbances · Forest restoration · Inverse modelling

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## Introduction

As an anemochorously dispersed pioneer tree species with a wide natural range throughout Eurasia, silver birch (*Betula pendula* Roth) has a high ecological value within temperate and boreal forest ecosystems (Atkinson 1992; Hynynen et al. 2010). Silver birches enhance soil nutrition and soil stability, provide watershed protection, act as structural elements with a long-term stabilizing effect, and provide habitats and food for many organisms (see Patterson 1993; Humphrey et al. 1998; Ferris and Humphrey 1999; Priha 1999; Beck et al. 2016). In some European countries, like England, Sweden, Finland and Latvia, silver birch is the most important broad-leaved tree species for timber production, plywood or veneer production (Cameron 1996; Luostarinen and Verkasalo 2000; Hynynen et al. 2010). Within their natural geographical range in Europe, birch species were often considered as a forest weed and, therefore, rigorously thinned out of forest stands during the last century (Röhrig and Gussone

1990; Koski and Rousi 2005). However, silver birch recently received renewed interest with respect to forest management at higher altitudes. The importance of silver birch in forest management has been increasing because of (a) the species' ability to promptly and extensively recolonize disturbed sites due to its high annual seed production and its fast juvenile growth, even in open areas with extreme climatic conditions (Perala and Alm 1990; Atkinson 1992; Zerbe 2001; Hynynen et al. 2010), and (b) the heightened risk of catastrophic events in central European spruce forests. The small winged nuts (1.5–2.0 mm) of birch are mainly dispersed by wind between June and November (Brouwer and Stählin 1975; Huth 2009). Pioneer forests composed of birches are able to quickly close water and nutrient cycles, thus soon creating a forest climate appropriate for the establishment of climax tree species (Zerbe 2009).

Therefore, empirical information about the seed production, seed dispersal distances, and deposited seed numbers of silver birch is required to establish 'precautionary' forest management systems that anticipate the high risk of catastrophic events, particularly in mountain spruce forests, and to ensure successful birch regeneration on disturbed sites. An approximate knowledge about the number of seeds per seed tree and the quality of the seed crop in a particular year is important to forecast the probability of natural regeneration in disturbed areas. The amount of seeds produced by an individual tree is influenced by, e.g. tree stem and crown dimension, vitality and age (Sarvas 1948, 1952; Moles et al. 2004) as well as by weather-dependent pollination and flowering success (Sarvas 1952). The allometric relationships between growth parameters and seed production per tree have been proven (Grisez 1975; Greene et al. 2004; Huth 2009; Da Ponte Canova 2018). Seed dispersal is an important driver for species movement, site colonization and the restoration of treeless or disturbed areas (Skarpaas et al. 2006), but can also produce limitations in spatial distribution of seeds (Daniels 2001; Karlsson 2001; Huth 2009).

It is generally difficult to determine the amount of produced seeds per tree and to study the process of seed dispersal (van Putten et al. 2012). For an exact determination of seeds per individual seed tree, cuttings would be necessary to count the seed numbers. For non-destructive methods, seeds must be marked or genetically analysed to link dispersed seeds to a specific seed source (van Putten et al. 2012; Nathan and Muller-Landau 2000; Tiebel et al. 2019). Therefore, phenomenological models are an appropriate statistical tool to predict seed dispersal, directionality and seed production on the basis of trapped seeds (Clark et al. 1998; van Putten et al. 2012). Huth (2009), who also used inverse modelling, reported mean seed dispersal distances (MDD) of 37 to 90 m for admixed silver birch trees within closed Norway spruce forests and seed production numbers of 0.18–7.3 million seeds per tree and

year. Other studies analysing the seed dispersal distances of *B. alleghaniensis* reported mean dispersal distances between 26.9 and 37.1 m (Clark et al. 1998; Greene et al. 2004). However, most studies on aspects of birch seed distribution have been conducted within closed forest stands (e.g. Skoglund and Verwijst 1989; Houle and Payette 1990; Graber and Leak 1992; Leder 1992; Houle 1998; Wagner et al. 2004; Huth 2009). Only few studies focused on the seed dispersal of birch in open areas or large gaps (Bjorkbom 1971; Hughes and Fahey 1988; Greene and Johnson 1996; Karlsson 2001).

As shown in different wind tunnel experiments, experimental results under controlled conditions cannot easily be transferred to real field conditions (Augsburger and Franson 1987; Johnson and West 1988, cited in Bakker et al. 1996; Kadereit and Leins 1988; van Dorp et al. 1996; Greene and Johnson 1997). This lack of transferability is caused by highly complex and variable environmental factors related to field conditions (e.g. wind conditions, site surface relief and ground vegetation cover or seed characteristics) (Fenner 1985; Okubo and Levin 1989; Skarpaas et al. 2006). Therefore, reliable information about the temporal and spatial patterns of seed rain in open areas is needed to assess the natural regeneration potential of *B. pendula* seedlings and to develop recolonization and restoration management strategies (see Zhao et al. 2016; Holmström et al. 2017). This applies particularly to the large wind thrown forest areas in central Europe, which were created by the storm events of the last decades (Gregow et al. 2017) and will probably become more and more frequent with progressing climate change (Möller et al. 2016).

The aim of this case study was to generate new knowledge about the dependence of seed distribution patterns on wind thrown sites on seed tree position in surrounding forest stands, seed tree numbers, seed crops, wind direction and topography. We observed the seed dispersal of *B. pendula* in 2015 and 2016 at two wind thrown forest sites at high altitudes (715–775 m a.s.l.) in Thuringia, Germany. (1) We used inverse modelling to predict mean dispersal distance, directionality and seed crop per seed tree of *B. pendula*, based on seed trapping data. (2) The dependence of predicted seed distribution patterns on relief inclination, wind direction, seed production per tree, seed tree number around the studied storm-felled sites as well as the position of the seed tree (valley, slope or plateau) could not be explained by inverse models. Therefore, we discussed these factors and their influence on the observed and predicted seed densities in the discussion section. Finally, (3) we used simulations to spatially optimize the positioning of the seed trees in relation to the studied sites with regard to optimal seed distribution in the open areas.

## Materials and methods

### Study area

The study area is located at high elevations and along the ridges of the Thuringian Forest, a mountain range in the federal state of Thuringia, Germany (50° 40' N and 10° 45' E). The area is situated between 400 and 982 m above sea level (a.s.l.), with a prevailing south-westerly exposition. The area is characterized by many slopes and an almost total absence of plateaus (Burse et al. 1997; Waesch 2003; Gauer and Aldinger 2005). The mean annual precipitation ranges from 800 mm in the south-west to 1200 mm along the ridges and falls to a level of 700 mm in the north-east (Burse et al. 1997; Gauer and Aldinger 2005; Bushart and Suck 2008). The annual average temperature in the region varies between 4 and 6 °C (Burse et al. 1997; Bushart and Suck 2008). The area is influenced by an Atlantic, moderately cool and moist central mountain climate (Burse et al. 1997; Gauer and Aldinger 2005). The prevailing winds are from the south-west, with a secondary wind maximum originating from the north-east. The average annual wind speed in the study area is 3.5–4.5 m s<sup>-1</sup> (Bürger 2003). The averaged meteorological data (based on half-hourly values) for the seed trapping periods of the presented study (2015 and 2016) are listed in Table 1. While no extreme events in wind speed were observed, the wind direction showed a high variability during the study periods.

The dominant soil types of the forest sites are low-base cambisols with low to medium nutrient contents (Gauer and Aldinger 2005). The regional landscape features a largely contiguous forest system with ~90% forest cover, some small upland meadows in stream valleys and occasional small raised bogs. The study area is dominated by single-layered, even-aged Norway spruce forests (*Picea abies* (L.) Karst.). Without anthropogenic influence, the potential natural vegetation would be dominated

by *Luzulo-Fagetum* and *Asperulo-Fagetum* beech forests (Frischbier et al. 2014).

We selected two study sites (B and E) 6 km apart from each other, located on slopes at higher elevations of the Thuringian Forest (715–775 m a.s.l.). Each site consisted of an open area surrounded by a forested search zone of 200 m (see 2.2). The open areas were wind thrown by the storm 'Kyrill' in January 2007 (Fink et al. 2009). Representative for the region, the stand conditions before the storm were dominated by 68–100 year-old Norway spruce. After the storm, the damaged areas were completely cleared, and no birch seed trees were present in the open areas. The size of the open areas was 4.0 ha and 12.7 ha, respectively (Table 2), and no closed regeneration layer had yet established at any of the study sites. The open areas were surrounded by 59–105 year-old Norway spruce forests admixed with a small number of adult isolated *Betula pendula* Roth, *Salix caprea* L. and *Sorbus aucuparia* L. trees.

Located along slopes, the choice of study sites allowed us to separately investigate uphill (site B) and downhill (site E) seed dispersal. The seed trees at site B were located in the valley at approximately 710–730 m a.s.l., and they were equipped with seed traps from the seed sources all the way to the uphill plateau at 760 m a.s.l. (Figure 1). At site E, seed trees were mainly found on a plateau (785–805 m a.s.l.) within a stand consisting of *Salix caprea*, *Sorbus aucuparia* and *B. pendula*, and seed traps were placed close to the seed sources on the upper slope (775 m a.s.l.) and downhill along the slope to the valley (675 m a.s.l.).

### Sampling design

Within the 200 m forested search zone at each study site, we mapped all *B. pendula* trees that were expected to potentially produce seeds ( $\geq 12$  cm diameter at breast height [dbh]; see Popadyuk et al. 1995; Roloff and Pietzarka 2010) using a blumax Bluetooth GPS-4013 Receiver. For each *B. pendula* tree, we recorded the dbh and

**Table 1** Aggregated meteorological data (based on half-hourly values; climate station 'Grosser Eisenberg'; 50° 37' 24" N and 10° 46' 59" O) of the 4-month seed-trapping periods in 2015 and 2016 in the study area

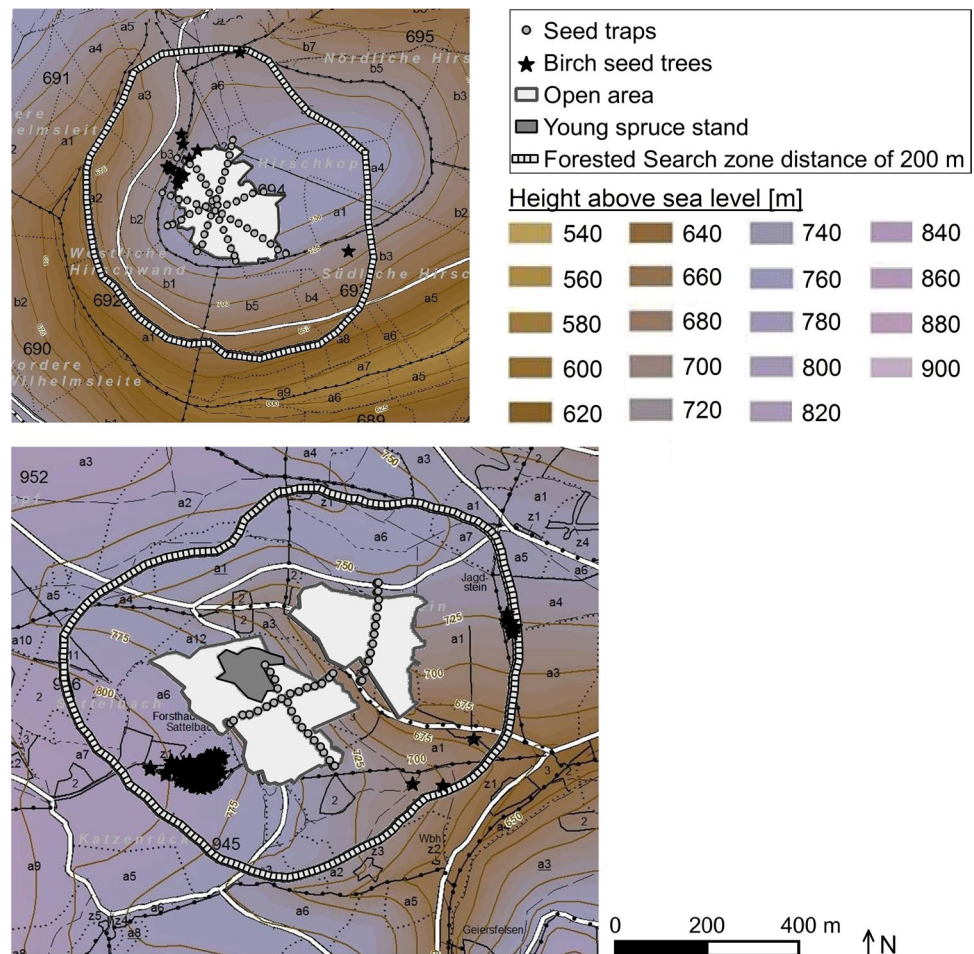
	2015					2016				
	From mid-Jul	Aug	Sep	Oct	Until early-Nov	From mid-Jul	Aug	Sep	Oct	Until early-Nov
Wind speed (m/s)										
Minimum	1.0	0	0	0	0.7	0	0.6	0	0	1.2
Maximum	7.2	8.3	9.9	4.6	4.4	4.7	5.2	6.4	6.5	3.5
Mean	3.6	2.9	1.8	2.0	2.4	1.8	2.2	2.1	2.3	2.5
SD	1.42	1.22	0.92	0.88	0.78	0.75	0.87	1.06	1.11	0.62
Wind direction (°)										
Mean	228	159	204	180	237	184	218	178	176	273
Median	253	181	235	214	233	226	250	206	222	283
SD	86.7	98.5	122.2	100.8	24.7	105.2	89.6	102.2	106.2	53.3
Mean temperature (°C)	11.1	18.2	9.8	6.0	9.9	17.7	14.9	14.4	5.1	3.8
Precipitation (mm/month)	0.6	65.2	74.3	NA	0.4	70.6	69.6	74.8	127.9	4.5

Please note that the data of July and November covers only studied days and not the entire month  
NA data not available due to measurement failures, SD standard deviation

**Table 2** Descriptive study site and birch seed tree data

Open area at study sites	B	E
Relief-induced dispersal	‘Uphill’	‘Downhill’
Elevation above sea level [m]	735–765	715–775
Topography	Mountain peak with slopes	Slopes
Size of open area [ha]	4.0	12.7
Number of seed traps [n]	54	41
Number of seed trees [n] within the 200 m forested search-zone around the open area [n]	16	83
Minimum distance between seed tree and seed trap [m]	12	74
Average Dbh of seed trees $\pm$ SD [cm]	31.1 $\pm$ 4.7	20.7 $\pm$ 4.4

*Dbh* diameter at breast high, *SD* standard deviation

**Fig. 1** Maps of the experimental study design at sites B (top) and E (bottom)

observed flowering in both years. The search zone distance of 200 m was chosen as a compromise between feasibility and prior knowledge of suggested effective birch seed dispersal distance in open and forested sites (Sarvas 1948; Karlsson 2001; Huth 2009). Sixteen and 83 seed trees with 24–42 cm and 13–37 cm in dbh were identified at sites B and E, respectively (Table 2).

At the study sites, we placed 54 (site B) and 41 seed traps (site E). Due to the vast areal extent of the open areas, seed traps were placed along two crossing line transects (site E) and four crossing line transects (site B), with intervals of 20 m between the traps, rather than along a regular grid (Fig. 1; see also Bjorkbom 1971; Greene and Johnson 1996). The orientation and length of the line transects were not

uniform, due to the differences in the size and shape of the two open areas. The line transects extended over the entire open area of each study site and into the surrounding Norway spruce forests. The minimum distances between the seed trees and the nearest seed trap were 12 and 74 m (Table 2).

The funnel-shaped seed traps had a diameter of 0.5 m and surface area of 0.196 m<sup>2</sup>. To ensure the functioning of the seed traps despite strong winds, a perforated plastic cup weighted with a stone was placed into each funnel-shaped net. The percolated plastic cups allowed rain water to runoff. The net funnels were fixed onto a bar 1 m above the ground. The traps were emptied periodically every 3 to 4 weeks and the number of seeds per trap was counted. The seed dispersal sampling periods each lasted 4 months from mid-July to early November in 2015 and 2016.

## Data analysis

Mean seed densities per m<sup>2</sup> were calculated for each seed trap across both study sites and years. Differences between seed densities at the two sites and between the two sampling years were analysed using the Mann–Whitney U-test, because the data were not normally distributed (Zar 2010). Significant differences were accepted at a *p* value of < 0.05. Furthermore, Quantum GIS (QGIS 2.4.0 Chugiak) was used to create maps of both study sites based on original forest maps and aerial orthophotographs. These maps were used to outline the boundaries of the open areas at each study site, to determine the surrounding 200 m forested search zone, and to mark the positions of seed trees and seed traps (Fig. 1).

## Seed dispersal model

A phenomenological model (provided as R-script) developed by van Putten et al. (2012) was used to investigate birch seed dispersal, including directionality (e.g. the effect of wind), the probability of seed deposition at certain distances from the seed source and a dbh-related prediction of seeds per tree and per year. The applied model is capable of accounting for the direction of seed dispersal by differentiating between isotropic and anisotropic dispersal kernels (see Eqs. 1 and 2). ‘Isotropic’ means that seed densities are equally dispersed in all azimuth directions, whereas ‘anisotropic’ dispersal accounts for a directional effect (e.g. due to wind) on seed density distributions (Wagner et al. 2004; Walder et al. 2009). Because of the above-mentioned model category, which is not mechanistic, the available meteorological data (Table 1) were only used to critically discuss the model results, for example the congruence of wind and seed dispersal direction as part of the anisotropic model.

We fitted seed shadows using the isotropic model and the anisotropic *no-shift* elliptic distorted-distance model with

the free parameters  $\beta$ ,  $\psi$  and  $\gamma$ . The most important algorithms were described by van Putten et al. (2012). To model the distance-dependent seed distribution (isotropic model), i.e. the ‘kernel’ of the model in the Cartesian coordinate system ( $x, y$ ), we used the negative exponential distribution as a density function ( $d(r_{(x,y)})$ , Eq. 1):

$$d(r_{(x,y)}) = \frac{e\left[-\frac{r_{(x,y)}}{\lambda}\right]}{r_{(x,y)} * 2\pi\lambda} \quad (1)$$

The dispersal distance within the negative exponential function is described by the parameter  $\lambda$ . The value  $r_{(x,y)}$  describes the distance between the position of the seed trees and seed traps using the Cartesian coordinates  $x$  and  $y$ , where seed density is known. To model the anisotropic dispersal, we combined the used ‘kernel’ function of isotropic model (Eq. 1) with the ‘distorted-distance function’ (Eq. 2). The ‘function’ transforms the isotropic (circular) contour lines into anisotropic (non-circular) contour lines (van Putten et al. 2012).

$$d(r_{(x,y)}) = \frac{e\left[-\frac{r_{(x,y)}}{\lambda}\right]}{r_{(x,y)} * 2\pi\lambda\beta\sqrt{\gamma^2 + 1}} \quad (2)$$

The parameter  $\beta$  (coherency) determines the flattening of the elliptic contour lines,  $\psi$  (rotation) describes the rotation of the elliptic contour lines around a seed tree along the common axis, and  $\gamma$  (drift) moves the centre of elliptic contour lines into a positive direction along the common axis (van Putten et al. 2012). Other models, e.g. lognormal, have been tested without improving the results. Additional information such as tree height, crown radius or shelter by neighbouring trees is not considered in this phenomenological model.

Isotropic and anisotropic seed dispersal was modelled separately for each study site (B and E) and year (2015 and 2016). The two study sites were split into the categories ‘uphill’ (B) and ‘downhill’ (E) on the basis of the relief-related seed dispersal. Inverse modelling was applied to fit the observed seed densities. The seed number modelled for each seed trap was calculated by summing the seed rain at a specific location relative to all seed trees. The mean dispersal distance (MDD) in the negative exponential kernel equals  $\lambda$ . In the case of isotropic modelling, the parameter equals  $MDD_{iso}$ . The fecundity of a seed tree  $\varphi$  was calculated using the following equation (Eq. 3):

$$\varphi = e^\alpha * dbh^2 \quad (3)$$

with  $\alpha$  as a fecundity parameter defining the allometric relationship between the dbh (mm) and the seed production of a tree. All parameters in the equations were simultaneously estimated by the provided R-script of the inverse models.

General references to isotropic and anisotropic inverse modelling can be found in Okubo and Levin (1989), Ribbens et al. (1994), Clark et al. (1999), Skarpaas et al. (2004), Wagner et al. (2004), Soubeyrand et al. (2007), Walder et al. (2009) and van Putten et al. (2012).

The parametric bootstrap approach, described by Faraway (2006) and Tekle et al. (2016), was used to compare the isotropic and anisotropic inverse model fits and to make a decision on the respective significance level. The likelihood ratio test (LRT) allows comparing models with different numbers of parameters by means of differences in log-likelihood between them. Bootstrap samples (data sets) were generated under a ‘null model’ (isotropic model) using the estimated parameters. The ‘null’ and ‘alternative models’ (anisotropic model) were then fitted based on these data sets and the LRT statistic was computed. This procedure was repeated 99 times for each study site and year. The differences in log likelihood between the isotropic and anisotropic models were used to derive an empirical distribution of LRT, where the null-hypothesis was true. The  $p$  value was estimated by comparing the empirical distribution of LRT to the observed values of LRT output (Faraway 2006; Tekle et al. 2016; Frischbier et al. 2019). Additionally, Akaike’s information criterion (AIC) provides information about differences between the statistical models. Spearman’s rank correlation coefficient including  $p$  value was used to test the goodness-of-fit (i.e. relation between the observed and predicted seed densities). All computations were performed using the R software version 3.3.2 (package: boot; R Core Team 2014).

### Simulations of seed dispersal scenarios

To apply our findings of seed dispersal in a practical context and to support silvicultural management decisions in the context of reforesting disturbed sites, two alternative scenarios of seed tree distribution were designed for study sites B and E, based on the area-specific seed dispersal model results with MDDs of 100 and 350 m, respectively. A regular distribution of seed trees on a 100 m grid surrounding the open areas (i.e. 30 trees) was compared with an aggregated seed tree distribution of the same tree numbers. The simulation was done for two conceptual forested sites with a size of 42 ha (700 m  $\times$  600 m) in which the two differently sized and shaped open areas from study sites B and E were integrated. All birch seed trees were assumed to have a reference dbh of 20 cm and to produce 1.5 million seeds as fitted by inverse modelling in 2016.

For analysing the scenarios, we could only consider the open areas, because the open area at site B represents a hill-top with only uphill seed dispersal (not the forested areas), and the sloped open area at site E forms a relief funnel which only represents downhill seed dispersal.

## Results

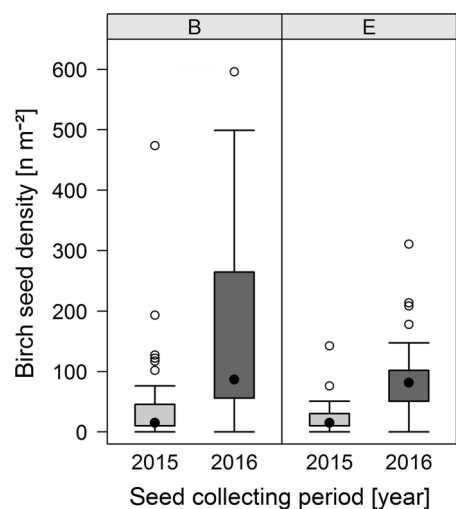
### Seed production

The densities of the deposited seeds in both open areas and surrounding forests were significantly higher in 2016 than in 2015 (Mann–Whitney  $U$ -test:  $p < 0.001$ ). Average seed densities ranged between 93 and 23  $\text{n m}^{-2}$  in 2015 and 445 and 86  $\text{n m}^{-2}$  in 2016 at sites B and E, respectively (Fig. 2). Overall, the recorded birch seed densities in traps were at least four times higher in 2016 than in 2015, with a maximum of 9557 (site B) and 311  $\text{n m}^{-2}$  (site E). In both years, birch seed numbers tended to be higher at site B, but this difference was not significant (Mann–Whitney  $U$ -test:  $p > 0.05$ ).

The allometric relationships between tree dbh and seed production for isotropic models were very tight. The fecundity levels (i.e. ‘ $\alpha$ ’ in Eq. 3) for the years 2015 (2.0–2.2) or 2016 (3.6) were relatively similar, indicating a slightly lower fecundity of seed trees in 2015. The expected seed production rate of the isotropic inverse model for a birch seed tree with a mean dbh of 20 cm was approximately 300,000–366,000 (2015) and 1,430,000–1,530,000 seeds per tree (2016) (Table 3). Birch seed trees with a dbh of 13–42 cm produced 0.14–1.5 million and 0.62–6.5 million seeds per tree in 2015 and 2016, respectively (Fig. 3).

### Spatial patterns and seed dispersal distances

The source tree-related pattern of cumulated trapped seed numbers followed a negative exponential function (Fig. 4).

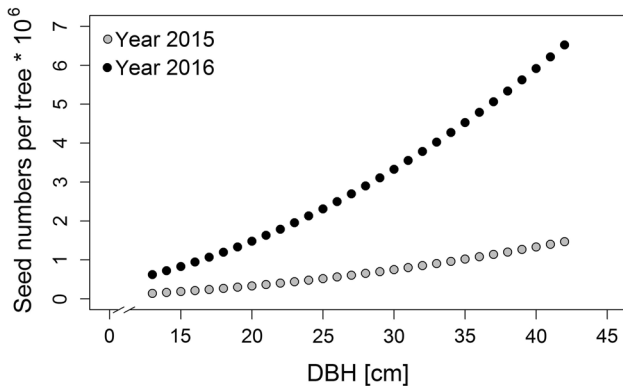


**Fig. 2** *Betula pendula* seed densities [ $\text{n m}^{-2}$ ] collected in 2015 and 2016 at study sites B and E. White circles show outliers and black circles inside the boxes are mean values. Differences between years at each study site are significant (Mann–Whitney  $U$ -test:  $p < 0.05$ )

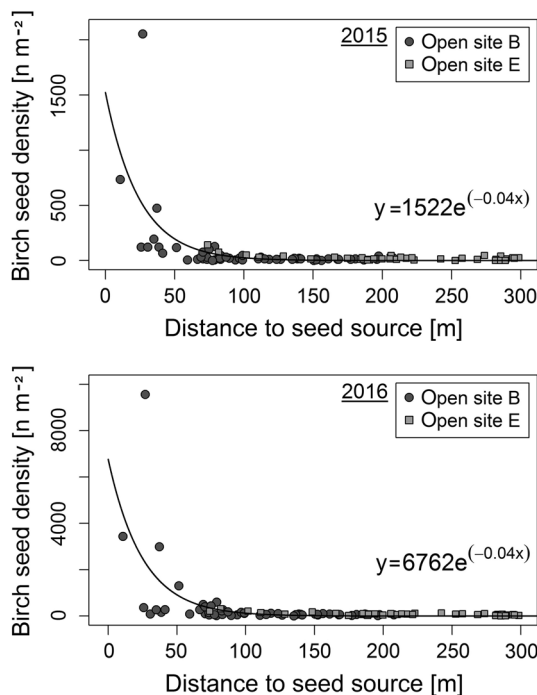
**Table 3** Inverse modelling results of isotropic and anisotropic dispersal (exponential function) of *Betula pendula* seeds for 2015 and 2016

Site	Year	Model	$\alpha$	$\lambda$	$\beta$	$\psi$	$\gamma$	AIC	loglike	rho	$p_{rho}$	$\varphi$	$p_{boot}$
B	2015	Isotropic	2.02	96.7	–	–	–	509.9	–253.0	0.522	0.000	0.30	0.22
		Anisotropic	2.15	430.6	0.065	–0.791	2.334	511.1	–250.5	0.602	0.000	0.34	
	2016	Isotropic	3.64	85.8	–	–	–	675.9	–335.9	0.636	0.000	1.53	0.88
		Anisotropic	3.71	136.4	0.791	0.490	1.029	667.2	–328.6	0.804	0.000	1.64	
E	2015	Isotropic	2.21	367.1	–	–	–	329.4	–162.7	0.463	0.002	0.37	1.00
		Anisotropic	1.30	234.9	0.005	0.888	185.673	337.2	–163.6	0.473	0.002	0.15	
	2016	Isotropic	3.57	379.8	–	–	–	413.7	–204.9	0.716	0.000	1.43	0.44
		Anisotropic	2.14	124.0	0.839	0.600	2.143	420.5	–205.3	0.812	0.000	0.34	

$\alpha$  fecundity,  $\lambda$  distance,  $\beta$  coherency,  $\psi$  rotation angle,  $\gamma$  drift, rho Spearman’s correlation coefficient between observed and predicted values,  $p_{rho}$  p value of Spearman’s correlation coefficient,  $\varphi$  seed production of a single seed tree with a dbh of 20 cm in millions,  $p_{boot}$  p value of bootstrap analysis



**Fig. 3** Isotropic inverse model predictions of seed production per seed tree depending on dbh (diameter at breast height) in 2015 and 2016



**Fig. 4** Complete set of measured *Betula pendula* seed densities [ $n\ m^{-2}$ ] at study sites B and E in 2015 and 2016 related to the distance from the seed source [m]. Note the different scales of the y-axes

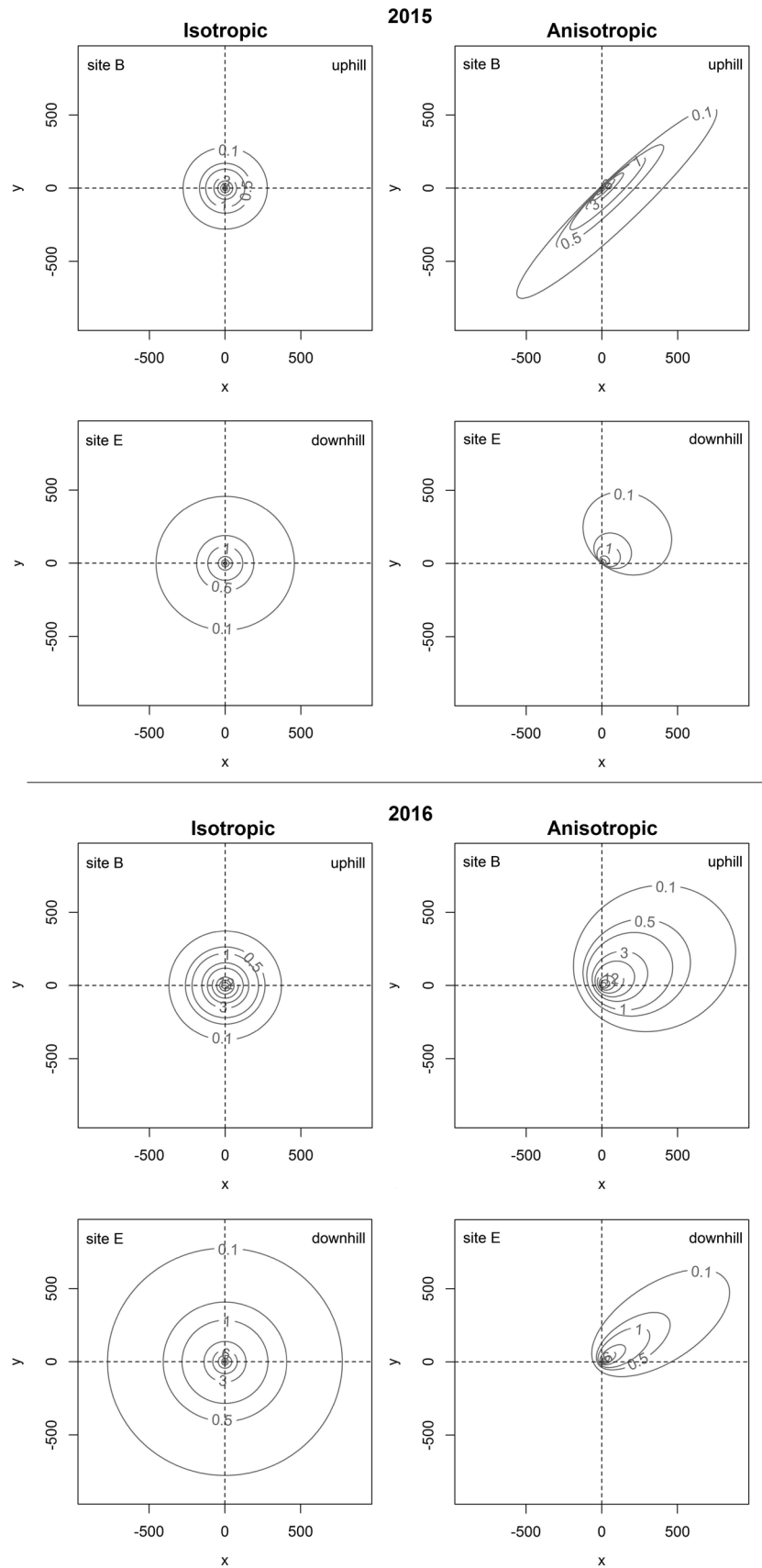
The highest seed densities at the study sites were found close to the seed sources, e.g. at the northern edge of the open area at site B or close to a stand of *Salix caprea*, *Sorbus aucuparia* and *B. pendula* within a spruce forest adjacent to the open area at site E (see Fig. 1). Seed densities decreased rapidly with increasing distance from the seed source. At a distance of 100 m from the seed sources, mean seed densities of only 24 and 41  $n\ m^{-2}$  were observed at site B (uphill dispersal) and E (downhill dispersal) in 2015, respectively, compared to 114 and 181  $n\ m^{-2}$  in 2016. During the same period, seed densities of only 15–25  $n\ m^{-2}$  were recorded downhill at a distance of 300 m from the seed sources at site E. In both years, the number of seeds trapped at the same distance from the seed source was slightly higher at site E compared to site B, which is, however, not visible through the overlapping lines in Fig. 4.

According to the isotropic model, the estimated uphill and downhill mean dispersal distances at site B and E were 97 (2015) and 86 m (2016) and 367 (2015) and 380 m (2016), respectively (Table 3; see left of Fig. 5).

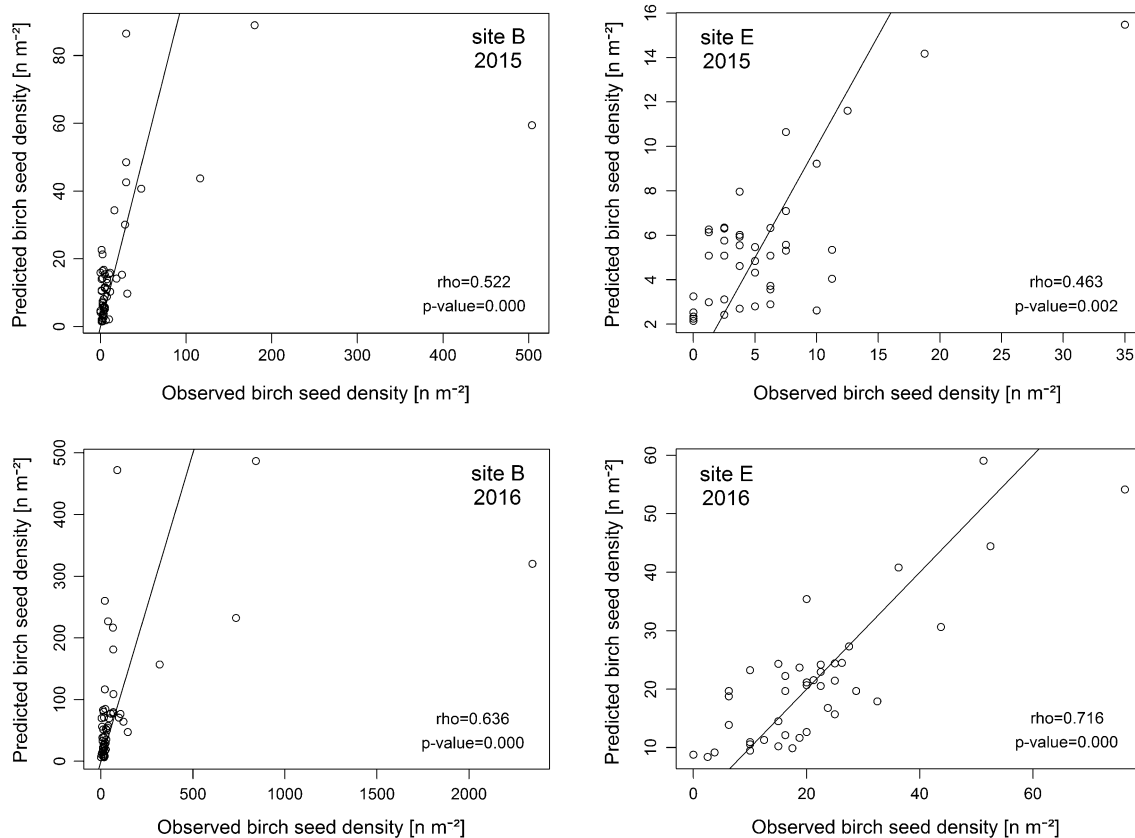
**Directionality**

The probability distribution of the seed dispersal distance of a single tree in the anisotropic models was quite similar to that of the isotropic models (Table 3), although the predicted seed shadows showed directional variation (Fig. 5). Values of  $\beta$ ,  $\gamma$ ,  $\psi$ , which characterize the spatial distribution of the anisotropic seed shadows, are listed in Table 3. However, the anisotropic models mostly featured higher AIC values than the isotropic models (with the exception of study site B in 2016), which indicates the anisotropic model as over-parameterized. The bootstrap statistic tests the hypothesis that the isotropic inverse model does not differ from the anisotropic model. The results of the bootstrap analysis for each year and study site also indicated that the anisotropic model was over-parameterized (bootstrap:  $p > 0.22$ ) and that the isotropic model was an appropriate approach for all sites and years (Table 3; Fig. 6).

**Fig. 5** Inverse model predictions of seed shadows [ $\text{n m}^{-2}$ ] simulated for a theoretical single *Betula pendula* seed tree with a dbh of 20 cm, given isotropic (left) and anisotropic (right) seed dispersal for study sites B and E in 2015 and 2016







**Fig. 6** Correlation plots of observed and predicted birch seed densities [ $n\ m^{-2}$ ] for study sites B and E in 2015 and 2016

### Simulations of seed dispersal scenarios

Based on the study results, scenarios of regular and aggregated seed tree distributions around the studied open areas were created to show that the distribution, the distance between seed trees and the disturbed sites, and the inclination have varying effects on the deposited seed densities.

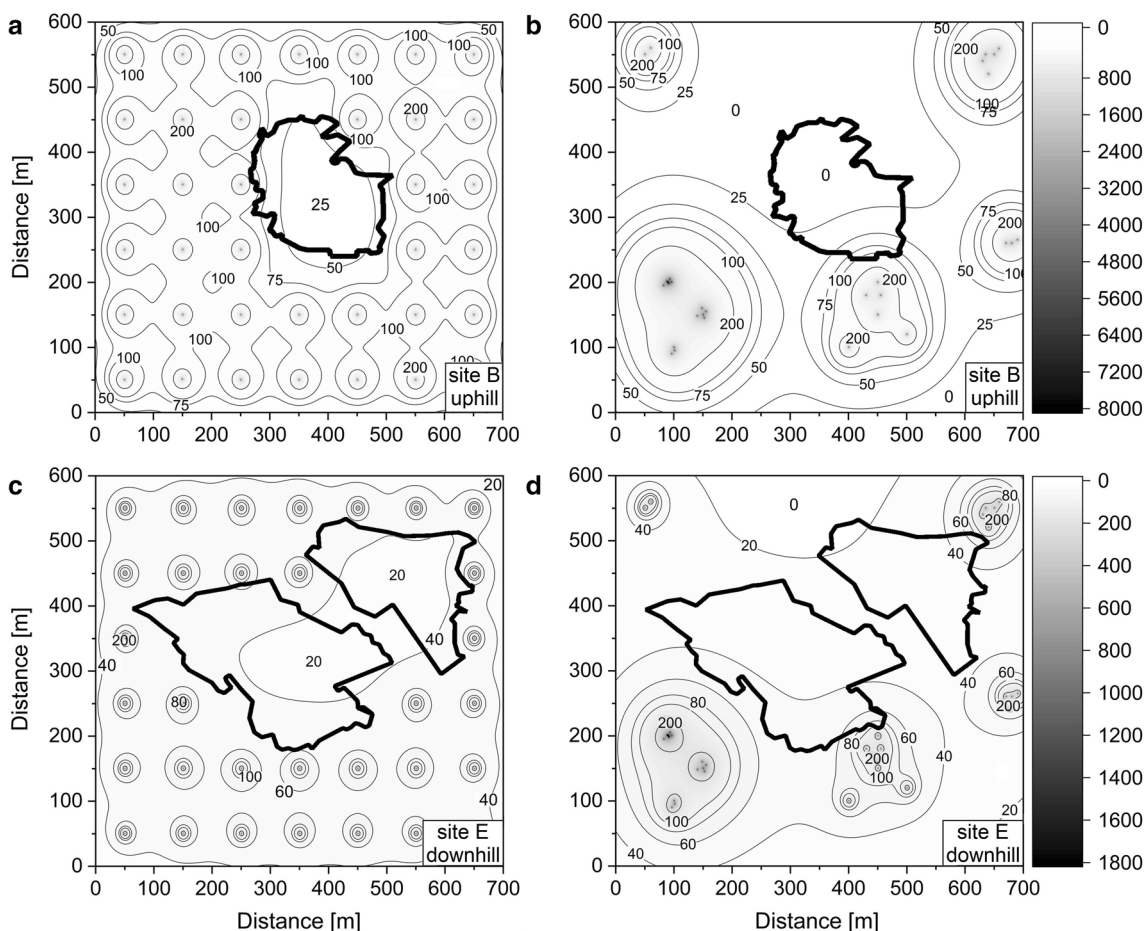
For an even, systematic seed tree distribution, the comparison of seed shadows between both sites showed higher deposited seed densities in the vicinity of seed trees at site B (Fig. 7a, c), because the same number of produced seeds are distributed uphill over smaller distances than downhill (see Fig. 5). However, in an undisturbed forest with a systematic seed tree distribution, there would be no areas without seed rain as the seed shadows of single seed trees would overlap at both sites. If disturbances interrupted the systematic seed tree grids—like observed at the studied storm-felled areas—and no seed trees were left in the disturbed area, approximately 20–25  $n\ m^{-2}$  birch seeds would still reach the hilltop (site B) and the valley (site E), independent of the inclination. It seems like there are no differences between sites, but the different sizes of the open areas must be considered. If the open area at site B

were to exceed the size of the open area at site E, the seed densities deposited in the open area would be considerably lower, which illustrates the aggregated distribution of the same numbers of seed trees (Fig. 7b, d). At distances of 5–250 m between the seed trees and the forest edges, the seeds dispersed uphill with the shorter MDD are not able to reach the entire open area at site B, but only the southern part. In contrast, the seed shadow of the seeds dispersed downhill from the aggregated seed trees at site E does not really differ from the spatial pattern of systematically distributed seed trees. At least 20  $n\ m^{-2}$  seeds are reaching almost all parts of the storm-felled area at site E with the exception of one small spot in the north.

## Discussion

### Seed production

There is solid evidence for strict allometric relationships between growth parameters, such as dbh, crown radius or basal area of a tree, and the individual seed crop of a tree (Grisez 1975; Greene et al. 2004; Huth 2009; Da Ponte



**Fig. 7** Isotropic seed shadow scenarios [ $n\ m^{-2}$ ] of simulated systematic (left) and aggregated (right) seed tree distributions of *Betula pendula* around the studied open areas at sites B (top) and E (bottom),

illustrated as bold lines. Note the different seed density scales for colour illustration in the figure panels

Canova 2018). The fitted fecundity parameter  $\alpha$  of the isotropic models for study site B and E was almost identical within each study year, which indicates a strong correlation between tree dbh and seed production, as previously assumed and confirmed for birch by Sato and Hiura (1998), Wagner et al. (2004) and Huth (2009). Therefore, the seed crop of birch trees of variable size can be easily estimated based on their dbh, if the seed production is not hampered by low viability or unfavourable weather conditions (see Grisez 1975). Birches with limited growing space, small crown projected areas and crown volumes have lower seed crops than large solitary individuals (Sarvas 1948). Nevertheless, Huth (2009) noted a restriction of these relationships. With the onsetting senescence of a tree, its seed crop progressively decreases while its diameter and crown dimension generally continue to increase. The strength of the relationship therefore decreases with progressing tree age.

The predicted seed production of a single birch seed tree in 2016 was four times higher than in 2015. Birch is known

for a large interannual variability in seed production (Sarvas 1948; Houle and Payette 1990; Kullman 1993; Huth 2009), which is mainly a response to the climatic conditions of the previous year (Kullman 1993; Holmström et al. 2017). On average, good seed years (i.e. so-called mast years) occur every 3 years (Sarvas 1948), during which the percentage of seed germination is significantly higher than in intervening (non-mast) years (Sarvas 1952; Bjorkbom 1971; Houle and Payette 1990). For a single silver birch, Denisow (2007, cited in Huth 2009) reported a seed production of 40,000–50,000 seeds in intervening years and 3.7–4.9 million seeds in a mast year. Compared to our study, significantly higher seed crops of individual trees with up to 7.3–10.0 million seeds (dbh of 24–80 cm) were reported by e.g. Arnborg (1948, cited in Perala and Alm 1990), Popadyuk et al. (1995), Wagner et al. (2004) and Huth (2009). In the present study, the slightly lower seed production of 0.6–6.5 million seeds per single seed tree (dbh of 13–42 cm) in 2016 was either a medium seed production year or a mast year. If it was a mast

year, the lower seed production numbers might have resulted from smaller birch tree crowns due to strong spruce competition and a lack of release thinning in the past.

### Spatial patterns and seed dispersal distances

As expected, the highest seed densities were observed close to the seed trees. At study site B, where birch seed trees were positioned at the edge of the open area, higher densities were observed up to distances of 40–50 m. Similar results were reported by Sarvas (1948), Fries (1984), Skoglund and Verwijst (1989) and Cameron (1996). In our study, the trapped seed numbers at site B decreased rapidly at distances exceeding 50 m (see Fig. 4). The seed distribution thus showed a negative exponential seed dispersal kernel, as Bjorkbom (1971), Hughes and Fahey (1988), Greene and Johnson (1996) and Karlsson (2001) previously reported for *B. alleghaniensis*, *B. pendula*, *B. pubescence* and *B. papyrifera*. In theory, one may expect a log-normal distribution of the distances the tiny and lightweight wind-dispersed seeds can travel (Stoyan and Wagner 2001; Huth 2009), but the majority of records in this study showed no peaks at specific distances from the seed trees (as in Greene and Johnson 1996; Stoyan and Wagner 2001; Huth 2009). A feasible explanation for this observation was given by Marquise (1969), who reported that primarily the heaviest and viable birch seeds were deposited close to the seed trees.

In the present study, seed dispersal distances within the sites were similar in both years regardless of the extent of seed production. Large differences of dispersal distances only occurred between the study sites. The modelled mean isotropic dispersal distances ( $MDD_{iso}$ ) of birch seeds distributed from the forest edge into the open area at site B were 86 and 97 m, as also detected by Wagner et al. (2004) and Huth (2009) for birch in level closed forest stands. In contrast, the  $MDD_{iso}$  of 367 and 380 m modelled for seed dispersal from within the adjacent spruce forest stands into the larger open area E indicated dispersal distances that were four times larger. Compared to the present study, Hughes and Fahey (1988), Daniels (2001) and Karlsson (2001) recorded lower dispersal distances of 30–125 m for *B. alleghaniensis*, *B. pendula* and *B. pubescens* in open areas.

Our very contradictory results of MDD are only comparable with studies from McEuen and Curran (2004), who found seed dispersal distances of *B. papyrifera* of 700 m between landscape fragments. The long distances were explained by an enormous seed tree presence (see also Zhao et al. 2016) and their extremely high seed production numbers. Similarly, we also had a huge seed source presence in the form of a mixed willow–rowan–birch stand at a distance of 74 m from the open area at site E (see Table 2;

Fig. 1). This potential explanation is further confirmed by Greene and Johnson (1996), Zhao et al. (2016) and Holmström et al. (2017) who mentioned that seeds are dispersed over larger distances if the size of the canopy opening increases, if seed source densities are located close to forest edges or if seed tree density is high. Therefore, to increase the probability of getting birch seeds onto storm-felled sites, an increasing number of seed sources would be needed at longer distances to the respective sites. Nevertheless, the few birch seed trees around the open area at site B were standing at the forest edge (see Fig. 1), making it actually more likely that seeds would disperse over larger distances than in closed forests (Holmström et al. 2017).

Thus, another effect should be considered: the relief, although this effect has not often been mentioned in previous studies. In this study, it seems that the dispersal distances of birch seeds decreased uphill (site B) or increased downhill (site E) depending on the inclination and seed tree position (valley, slope or plateau) relative to the storm-felled site. Hill and Stevens (1981), who studied soil seed banks, found a 30 m shorter distance for uphill deposition of birch seeds than for downhill deposition. Based on the estimated  $MDD_{iso}$ , we may therefore assume a strong effect of inclination on the dispersal distance of birch seeds. However, the two study sites were not selected rigorously enough to test for inclination effects. Therefore, the results should be conservatively interpreted. Some of the other aforementioned factors, e.g. differently sized open areas, seed tree densities and distances between seed sources and forest edges, may also have influenced the dispersal distances. Consequently, the documented results of this case study are not as such directly transferable to all forest areas.

The distance of long dispersal is particularly determined by secondary dispersal (Matlack 1989; Greene and Johnsons 1997), but this factor can be neglected in the present study due to similar ground vegetation cover and thus likely similar secondary dispersal in both open areas. Based on our data, we have no chance to check for secondary seed dispersal in any way.

### Directionality

Due to non-random anemochorous seed dispersal, previous studies often showed directionality for birch seed dispersal (Wagner et al. 2004; Wright et al. 2008; Huth 2009). However, this was not clearly confirmed by results of the present study. An explanation for the surprising isotropy of seed dispersal in this study might be the relatively long seed collection periods (4 month). The variability of wind directions and wind speeds occurring during a period of 4 months—boosted and modified by turbulence and varying wind speeds in the open areas due to vegetation cover and

structure (see Moon et al. 2013)—may explain the lack of observed anisotropy. While the half-hourly meteorological data (Table 1) showed no extreme wind events during the two study periods, with a maximum wind speed of  $9.9 \text{ m s}^{-1}$ , the monthly mean wind direction featured high standard deviations of  $\pm 25$  to  $\pm 122^\circ$ . On some days during the study periods, the variability of the wind direction was as high as  $\pm 206^\circ$ . The observed isotropic distributions are thus plausible, because no prevailing wind direction was identified for either study period and birch seeds were dispersed in a variety of directions. The assumption that the anisotropic models reveal a better fit to the empirical 4-month data was therefore rejected. Houle and Payette (1990) found anisotropic spatial patterns of the seed shadows of *B. alleghaniensis* after subdividing the seed rain period into shorter study periods. If we had chosen shorter periods for emptying the seed traps in this study (e.g. 14 day periods), we might have also been able to detect anisotropy by inverse modelling (Wagner et al. 2004).

However, short-term analyses of 14 day periods would not be useful for deriving silvicultural recommendations, because in this context the entire period of seed rain, i.e. 3–4 months in summer and autumn, has to be considered. For silvicultural practice, it is important to know that equally distributed seed rain can be expected around seed trees if strong wind regimes with variable wind directions prevail at a specific site.

### Simulations of seed dispersal scenarios

The abundance and the spatial pattern of potential seed trees near a particular disturbed site are important determinants upon which forest managers could base silvicultural decisions about risk-adapted reforestation concepts and preventative risk-adapted seed tree management.

The seed dispersal scenarios for silvicultural management decisions showed that in case of a systematic, even seed tree distribution, inclination differences are not clearly affecting the seed shadow, and known limits of birch dispersal distances (MDD) can generally be compensated, especially for uphill seed dispersal. However, if seed trees are aggregated and unevenly distributed, the effect of the inclination is clearly visible in the resulting seed shadow. In the latter case, the inclination has an important influence on the regeneration success of storm-felled sites in addition to the distance between the seed sources and the open area as well as the number of seed trees or tree groups.

### Recommendations of silvicultural management decisions

For the practical management of regenerating disturbed sites, it can be concluded that seed dispersal is very sensitive to the distribution, the number and loss of seed trees in nearby forests as well as the size and inclination of disturbed areas. Hence, Willis et al. (2016) highlighted the importance of local seed source availability for successful birch regeneration. Sarvas (1948) mentioned that at least 100 to 200  $\text{n m}^{-2}$  of viable seeds are necessary for successful regeneration and recommends a density of 4 to 8  $\text{n ha}^{-1}$  of *B. pendula* seed trees, whereas Safford and Jacobs (1983) advocate a seed tree number of 7 to 12  $\text{n ha}^{-1}$  for *B. papyrifera*. Based on Sarvas's (1948) minimum recommendation of 100 seeds  $\text{m}^{-2}$ , we can also give recommendations on the required seed tree numbers in forests. Derived from the uphill and downhill mean dispersal distances and the deposited seed numbers at study sites B and E (cf. Figure 4 and 7), 4 and 16  $\text{n ha}^{-1}$  seed trees are needed under unfavourable conditions, e.g. in non-mast years. This corresponds to seed tree grid intervals of 60 and 30 m, respectively. For small groups of trees, the distance can be slightly larger, as illustrated in Fig. 7. Higher source tree numbers are needed for ensuring the natural regeneration of disturbed sites if the present seed trees produce insufficient seed crops as a result of lacking tending measures. Thus, the aforementioned seed tree numbers should be considered as minimum numbers.

However, with respect to uphill dispersal, we assume that areas with insufficient numbers of deposited seeds will probably always occur in disturbed sites, unless the area is completely surrounded by seed trees. In case of disturbed sites of more than 4 ha, it is thus impossible to ensure a full cover of natural birch regeneration due to the limited seed dispersal distances. The natural regeneration of such large areas should therefore be supported by additional reforestation measures. In addition, seed trees surviving after a disturbance event must not be removed from the disturbed sites and seed trees in the vicinity of the sites should be promoted and vitalized wherever possible. Advance regeneration, which established underneath the canopy prior to the disturbance event, can also provide valuable benefits for regenerating disturbed sites. For the regeneration of small disturbed areas, which usually occur more frequently (Brang et al. 2015), risk-adapted forest management should include the 'spatial optimization' of birch seed trees within conifer forests, due to the limited dispersal distance of birch seeds in general. A few groups of aggregated seed trees within a

forest stand or some seed trees along the forest edge and forest roads in otherwise pure conifer forests are not sufficient for regenerating disturbed areas, but can be a good initial for the integration of birch trees in conifer forests. Along forest roads, paths or trails, birch trees have the possibility of unrestricted crown growth on one side and thus feature a more proliferous seed production. However, a network of more or less regularly distributed individual birches is needed within conifer forests, preferably even of small groups of seed trees, because silvicultural measures are easier to implement (see Cameron 1996; Hynynen et al. 2010) and the chances of successfully regenerating more distant sites is higher. For birches, Cameron (1996) mentioned required thinning intervals of 5–7 years for ensuring a good crown growth. Conservation, vitalization and propagation are important factors for annual birch seed crop quality and quantity, which makes more sense for tree groups than for single trees due to costs and the regulation of interspecific competition.

## Conclusions

To ensure successful regeneration, reliable empirical information concerning seed production and seed dispersal distances are necessary. Inverse modelling was applied to fit seed distribution and seed production on the basis of observed seed densities.

The findings of our case study indicated a strong influence of (1) site inclination, (2) seed tree position (valley, slope or plateau) and distance to a storm-felled site on the seed dispersal of *B. pendula*. The seed shadow of birch trees is also influenced by (3) the number of seed sources. In the context of natural *B. pendula* regeneration on disturbed sites, it must be noted that seed dispersal is spatially limited compared to other anemochorous tree species such as *Salix* spp. (Gage and Cooper 2005; Tiebel et al. 2019). However, in light of the specific characteristics of the selected study areas, the transfer of the presented results to other sites and regions should be cautious.

For the practical management of regenerating disturbed sites, it can be concluded that seed dispersal is very sensitive to the distribution, the number and loss of seed trees in nearby forests as well as the size and inclination of disturbed areas. Therefore, risk-adapted forest management should include the ‘spatial optimization’ of birch seed trees, ideally creating a network of small seed tree groups scattered more or less regularly within pure conifer forests.

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## Compliance with ethical standards

**Conflicts of interest** The authors declare that they have no conflict of interest.

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