

Article

Mortality of Boreal Trees

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Abstract: A dataset collected from central South Finland was used to investigate the mortality of boreal trees. The mortality rate was found to be the order of three times that predicted by earlier Nordic mortality models, being in the upper range of international literature observations. Small subpopulations of any tree species tend to die out. The mortality of downy birch increases with stand basal area, as well as with stand age. The mortality of Norway spruce and silver birch increases after 100 years, while that of Scots pine is invariant to age. It is suspected that the high mortality of conifers is due to climatic phenomena of anthropogenic origin. As the relative loss rate of basal area is insensitive to stand basal area, the mortality of trees does not strongly regulate thinning practices, but stand-replacing damage can be avoided by retaining a larger timber stock, along with an enhanced proportion of deciduous trees.

Keywords: *Picea abies*; *Pinus sylvestris*; *Betula pendula*; *Betula pubescens*; logistic regression

1. Introduction

It is customary to divide reasons for the mortality of forest trees into stand dynamics, on the one hand, and external factors, on the other. The internal dynamics of a stand induce a self-thinning process [1–3], whereas external factors may induce mortality even if within-stand competition would not [4,5]. The self-thinning rate may greatly depend on the initial stand density, or the development stage of any stand [4]. To account for the self-thinning process, any mortality model must contain some measure of stand density [6–8]. The tree status contribution to mortality also appears to depend on stand status [9]. The mortality time rate also probably depends on site fertility and other variables contributing to the forest growth rate [1,2,10–13]. On the other hand, the growth rate of an individual tree correlates negatively with mortality [14]. Decrement in net primary productivity predicts increasing mortality [15]. Aging senescence, as such, may also contribute [16]. Volume mortality rates are often smaller than mortality rates on a stem count basis [17].

External factors typically induce fluctuations in the mortality rate [18]; trends in external circumstances also induce trends in tree mortality, probably interacting with stand internal dynamics [4,19–22]. The interaction with stand dynamics induces a contribution of stand structure and relative position of any tree within the stand [23]. Similarly, the mortality allocation within any self-thinning process depends on stand structure and tree position, possibly also stand history [2]. Thinnings accelerate wind damage [24–28], whereas snow damage tends to concentrate on non-dominating trees [25,29].

A third view to tree mortality is the effect of severe disturbances. In the Pacific Northwest, stand-replacing disturbances have been reported due to wildfires exclusively [30]. Recent severe disturbances in Europe have instead been due to combinations of drought and bark beetles [31–35] or windfall and bark beetles [36,37]. Drought–pathogen interactions have been reported from Central United States [38]. Non-stand-replacing disturbances were divided to endogenous (pathogens and insects) and exogenous (fire, wind, and landslide) origins, the latter appearing less frequently but more severely [30]. However, mortality patterns, driven by endogenous and exogenous factors, apparently evolve over time [31–34,36,37,39–41].



Citation: Kärenlampi, P.P. Mortality of Boreal Trees. *Sustainability* **2024**, *16*, 6370. <https://doi.org/10.3390/su16156370>

Academic Editor: Ali Ayoub

Received: 16 April 2024

Revised: 11 June 2024

Accepted: 22 July 2024

Published: 25 July 2024



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The objective of this study was to investigate the mortality factors and mortality rate of boreal forest trees. For this purpose, empirical materials from central South Finland was used, and the outcome was compared with literature observations.

2. Materials and Methods

Initially, 11,299 living trees were observed on 106 experimental plots, of which 2609 were Scots pine (*Pinus sylvestris*), 6748 Norway spruce (*Picea abies*), 1214 silver birch (*Betula pendula*), and 728 downy birch (*Betula pubescens*). The experimental plots were located close to the Helsinki University field station Hyytiälä, located between 150 and 180 m above sea level. All plots contained a mixture of tree species. Any tree was identifiable by a tree code assigned during the first observation. The plots were re-observed after a time interval from three to six years; 2166 trees were observed after three years, 3144 after four years, 2848 after five years, and 3191 after six years. Correspondingly, there were four different time intervals for mortality observation. Any tree with green foliage during the growing season was considered living, and any tree without green foliage was considered dead. The observations, made using manual calipers, were started in the year 2007 and terminated in the year 2014. For the four different time intervals, the number of measured trees, as well as the number of dead trees, is shown in Table 1. One can calculate from Table 1 that the average gross mortality rate was 12.0% for Scots pine, 10.2% for Norway spruce, 5.7% for silver birch, and 8.8% for downy birch. The annual average mortality rates, resulting from a logarithmic conversion, were 2.4% for Scots pine, 2.4% for Norway spruce, 1.2% for silver birch, and 1.9% for downy birch.

Table 1. The number of observed trees, as well as the number of trees dying within the observation interval, for four observation intervals and four tree species.

Measurement Interval					
3 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
	Species code	1	2	3	4
Number of trees		460	1286	217	153
Number of dead trees		9	56	5	3
Measurement Interval					
4 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
	Species code	1	2	3	4
Number of trees		499	1950	549	147
Number of dead trees		36	166	11	15
Measurement Interval					
5 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
	Species code	1	2	3	4
Number of trees		639	1854	171	184
Number of dead trees		60	190	25	21
Measurement Interval					
6 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
	Species code	1	2	3	4
Number of trees		1011	1659	277	244
Number of dead trees		208	280	28	25

Descriptive statistics of the present materials are given in Table 2. It was found that the trees mostly appeared in wooded stands: the mean value of the basal area for any tree species was above 25 and the stem count above 1100/ha. The tree diameters indicate that even if some saplings have been included, the measured trees have mostly been of commercial size.

Table 2. Descriptive statistics of the material.

	Tree Diameter	Stand Basal Area	Basal Area of Larger Trees	Basal Area Increment Rate	Stem Count [1/ha]	Age
	[mm]	[m ² /ha]	[m ² /ha]	[m ² /(ha*a)]		[a]
<i>Pinus sylvestris</i>						
min	48	14.5	0.1	0.08	352	20
max	583	75.1	67.5	1.54	3016	161
mean	216	29.5	15.5	0.59	1160	60
stdev	86	11.6	10.4	0.20	587	30
<i>Picea abies</i>						
min	24	14.5	0.0	0.08	340	10
max	996	75.1	75.1	1.54	2892	150
mean	172	29.5	22.9	0.59	1211	66
stdev	85	11.6	12.4	0.24	615	29
<i>Betula pendula</i>						
min	29	13.7	0.1	0.08	340	10
max	459	75.1	70.6	1.54	2892	137
mean	182	27.5	17.3	0.57	1152	50
stdev	70	10.5	11.5	0.20	570	20
<i>Betula pubescens</i>						
min	38	13.7	0.4	0.08	340	17
max	280	75.1	75.1	1.38	2711	132
mean	129	26.0	20.8	0.62	1334	48
stdev	55	9.4	9.7	0.19	660	17

For any observation interval, there is a binary distribution of tree survival status. Correspondingly, a logistic regression was fitted separately for the data from any observation interval, and for any tree species. The logistic regression function parameters were fitted by minimizing the cost function:

$$-\frac{1}{N} \sum_{i=1}^N \{y_i \log[p(y_i)] + (1 - y_i) \log[1 - p(y_i)]\} \quad (1)$$

where N is the number of observations, y_i is the observation outcome, and $p(y_i)$ is the mortality probability predicted by the logistic regression. The fitted logistic function was of the following form:

$$p(y_i) = \{1 + \exp[(-1)(a_0 + a_1x_1 + \dots + a_nx_n)]\}^{-1} \quad (2)$$

where x_i represents independent variables, and a_i represents coefficients to be fitted. In the most simple form, one independent variable was examined in Equation (2), while the

most complex case investigated contained three explanatory variables, even though not necessarily mutually independent.

As the data contain observations with four distinct observation intervals, there is a need to unify the results. The mortality probability within a finite time interval can be converted into an annual mortality probability as follows:

$$a(y) = \frac{\ln[1 - p(y)]}{-\Delta t} \quad (3)$$

where Δt is the time interval between observations.

Even if Equation (3) gives annual mortalities, the results differ between the different observation intervals since the datasets differ. A master curve for any tree species, as a function of any explanatory variable, can, however, be constructed as an appearance-frequency-weighted average of the annual mortalities from the different datasets.

There is an alternative method for the determination of mortality based on a dataset with varying observation intervals [42]. Instead of modeling mortality, the survival probability was modeled as follows:

$$p(z_i) = \{1 + \exp[(-1)(a_0 + a_1x_1 + \dots + a_nx_n)]\}^{-t} \quad (4)$$

where t is the number of observation periods, and the annual survival probability is gained by raising Equation (4) to the power of $1/t$. Then, the annual mortality estimate is given as follows:

$$a(y) = 1 - [p(z)]^{1/t}. \quad (5)$$

In addition to the mortality probability of individual trees predicted in terms of a logistic function, the loss rate of basal area due to mortality was investigated on the stand level. More specifically, the change in stand basal area is given as follows:

$$\Delta BA = BA(\tau_2) - BA(\tau_1) = \int_{\tau_1}^{\tau_2} \frac{dBA}{dt} dt = \int_{\tau_1}^{\tau_2} \left[\left(\frac{dBA}{dt} \right)_g - \left(\frac{dBA}{dt} \right)_m \right] dt \quad (6)$$

where $\left(\frac{dBA}{dt} \right)_g$ is the basal area increment rate in living trees, and $\left(\frac{dBA}{dt} \right)_m$ is the basal area loss rate due to trees deceasing. The expected value of any basal area change rate is as follows:

$$\left\langle \left(\frac{dBA}{dt} \right)_i \right\rangle = \int_{\tau_1}^{\tau_2} \left(\frac{dBA}{dt} \right) p(t) dt \quad (7)$$

where $p(t)$ is the probability density of time.

As the accumulated loss was determined within a period from three to six years, the annual BA loss rate was determined using Equation (3).

3. Results

3.1. Mortality Model Results

Table 3 shows the minimized values of the cost function (1) for the logistic function (2) containing three single explanatory variables, two explanatory variables together, and then three explanatory variables together, the three not being mutually independent. With a single explanatory variable, the minimized cost function values display a qualitative ranking: the stand basal area (BA) does not provide the smallest value of the cost function in any case. The minimum cost function values with one explanatory variable are distributed between the tree diameter (D) and basal area of larger trees (in diameter) within the stand (BAL).

Table 3. a. Minimized values of the cost function (1) for four tree species and seven sets of explanatory variables in Equation (2), for a measurement interval of three years. Bolded numbers indicate the minimum values of the cost function within any group of explanatory variables. b. Minimized values of the cost function (1) for four tree species and seven sets of explanatory variables in Equation (2), for a measurement interval of four years. Bolded numbers indicate the minimum values of the cost function within any group of explanatory variables. c. Minimized values of the cost function (1) for four tree species and seven sets of explanatory variables in Equation (2), for a measurement interval of five years. Bolded numbers indicate the minimum values of the cost function within any group of explanatory variables. d. Minimized values of the cost function (1) for four tree species and seven sets of explanatory variables in Equation (2), for a measurement interval of six years. Bolded numbers indicate the minimum values of the cost function within any group of explanatory variables.

a.					
Measurement Interval					
3 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
Explanatory variable		1	2	3	4
D		0.04179	0.07725	0.03989	0.04121
BA		0.04108	0.07772	0.04762	0.03650
BAL		0.04031	0.07776	0.04477	0.03589
D + BA		0.03999	0.07725	0.03987	0.03513
D + BAL		0.04031	0.07706	0.03900	0.03242
D + D ² + BA		0.03948	0.07702	0.03932	0.03475
D + D ² + BAL		0.03975	0.07683	0.03791	0.03242
b.					
Measurement Interval					
4 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
Explanatory variable		1	2	3	4
D		0.10962	0.12640	0.03364	0.14173
BA		0.11101	0.12599	0.03788	0.14215
BAL		0.10754	0.12420	0.03230	0.13582
D + BA		0.10894	0.12594	0.03210	0.14000
D + BAL		0.10742	0.12360	0.03102	0.13542
D + D ² + BA		0.10888	0.12590	0.02953	0.13972
D + D ² + BAL		0.10740	0.12338	0.02926	0.13459
c.					
Measurement Interval					
5 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
Explanatory variable		1	2	3	4
D		0.12772	0.13962	0.15299	0.14007
BA		0.13415	0.14353	0.18063	0.15359
BAL		0.13442	0.14066	0.16593	0.14958
D + BA		0.12704	0.13933	0.15287	0.14004
D + BAL		0.12752	0.13836	0.15231	0.14000

Table 3. Cont.

c.					
D + D ² + BA		0.12502	0.13928	0.14967	0.13943
D + D ² + BAL		0.12506	0.13831	0.14947	0.13950
d.					
Measurement Interval					
6 years	Tree species	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
Explanatory variable		1	2	3	4
D		0.21055	0.19007	0.11696	0.14206
BA		0.21948	0.19694	0.14221	0.14036
BAL		0.21501	0.19731	0.13644	0.13792
D + BA		0.20866	0.19001	0.10519	0.13889
D + BAL		0.20556	0.19000	0.10473	0.13791
D + D ² + BA		0.20750	0.18021	0.10497	0.13136
D + D ² + BAL		0.20462	0.18022	0.10445	0.12975

It can be found from Table 3 that as increasing the number of explanatory variables always reduces the achievable minimum value of the cost function (1), the decrement is not very large. Correspondingly, depending on the purpose, any version of Equation (2), as evaluated in Table 3, may be useful. This fact is here utilized to demonstrate the effects of the explanatory variable in terms of single-variable logistic models (2).

Figure 1 shows the appearance density-weighted representative master curve for annual mortality for the four tree species as a function of breast-height diameter. Generally, mortality is reduced as a function of increasing diameter. At small diameters, the mortalities of Scots pine and silver birch are the greatest. Norway spruce and downy birch are less sensitive to stem diameter, and at high diameters, the annual mortality of Norway spruce is the highest of the tree species.

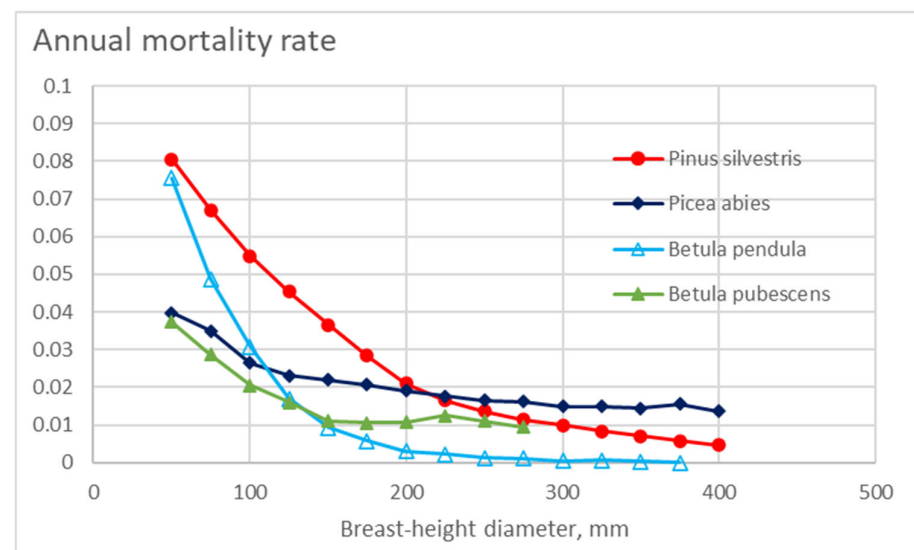


Figure 1. Annual mortality rate in different diameter classes for the four tree species, as a function of tree diameter.

Figure 2 shows the appearance density-weighted representative master curve for annual mortality for the four tree species as a function of stand basal area. Generally,

mortality is increased as a function of increasing stand basal area. The effect, however, is much weaker than that of the tree diameter in Figure 1.

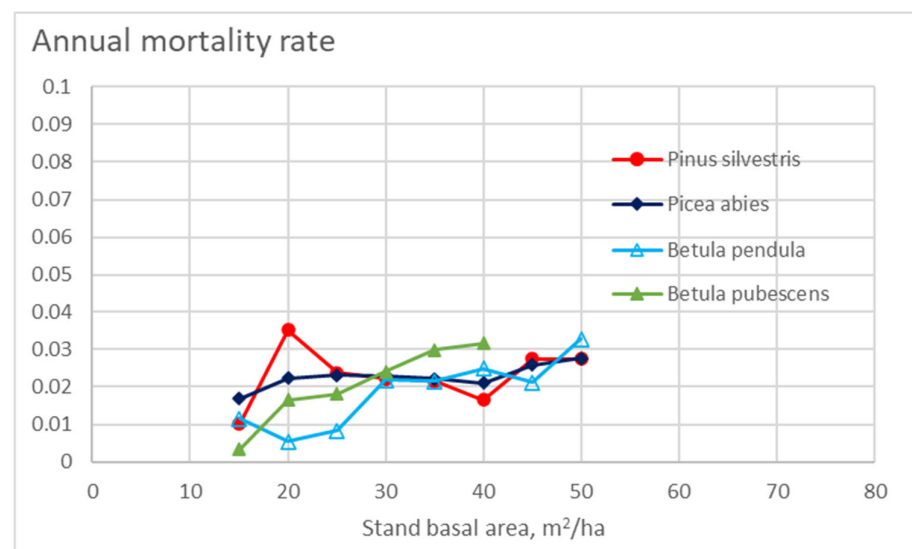


Figure 2. Annual mortality rate in different stand classes for the four tree species, as a function of stand basal area.

Figure 3 shows the appearance density-weighted representative master curve for annual mortality for the four tree species as a function of the basal area of larger trees within the stand. The mortality increases as a function of the increasing stand basal area of larger trees, and the effect is stronger than that of the stand basal area in Figure 2. In Figure 3, the effect of the basal area of larger trees is stronger for birch species than in the case of conifers.

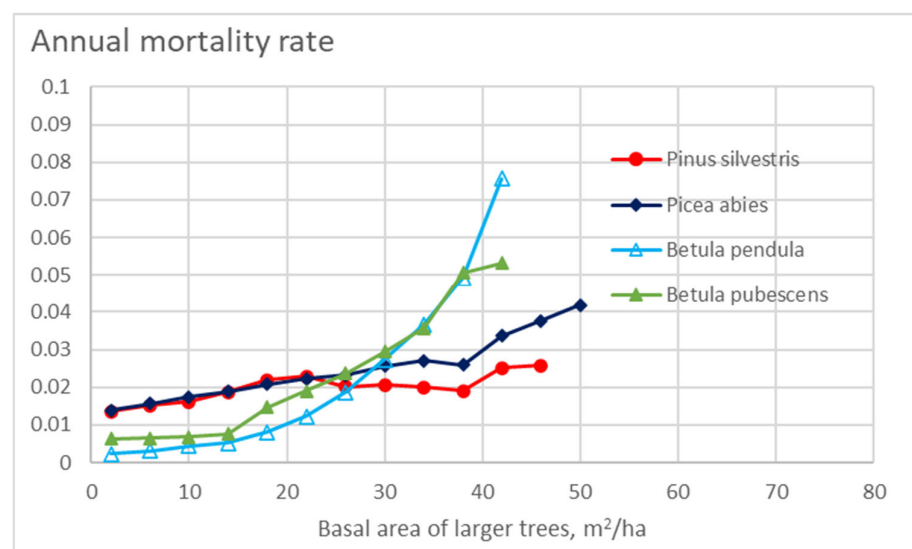


Figure 3. Annual mortality rate in different stand classes for the four tree species, as a function of the basal area of larger trees on the stand.

Figure 4 shows the appearance density-weighted representative master curve for annual mortality for the four tree species as a function of three explanatory variables: the breast-height diameter, the square of the breast-height diameter, and the basal area of trees on the stand. The figure has only one explanatory variable. The squared diameter, however, is included in the modeling result (Equation (2)). The third variable was taken as a mean-

field approximation, as the expected value of the stand basal area for any tree species and breast-height diameter class. It was found that mortality decreases with increasing tree size, even if downy birch shows a non-monotonic behavior. In accordance with Figure 1, the annual mortality of Norway spruce is the least sensitive to tree size, and at high diameters, the annual mortality of Norway spruce is the highest of the tree species.

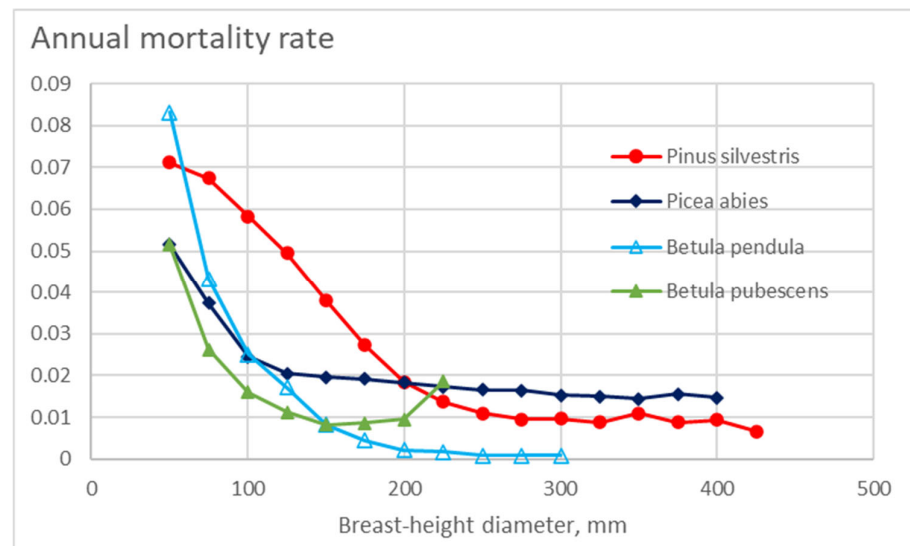


Figure 4. Annual mortality rate in different diameter classes for the four tree species, within a model with three independent variables, where the stand basal area is included as a mean-field approximation, according to Equation (3).

As the results shown in Figure 4, depending on the expected value of the stand basal area within any tree species and diameter class, the expected basal area values are of interest. They are shown in Figure 5. It was found that the basal area expected values have been mostly below 30 m²/ha in the case of birch species, above 30 m²/ha in the case of spruce trees. In the case of pine trees, the basal area increased as a function of tree size.

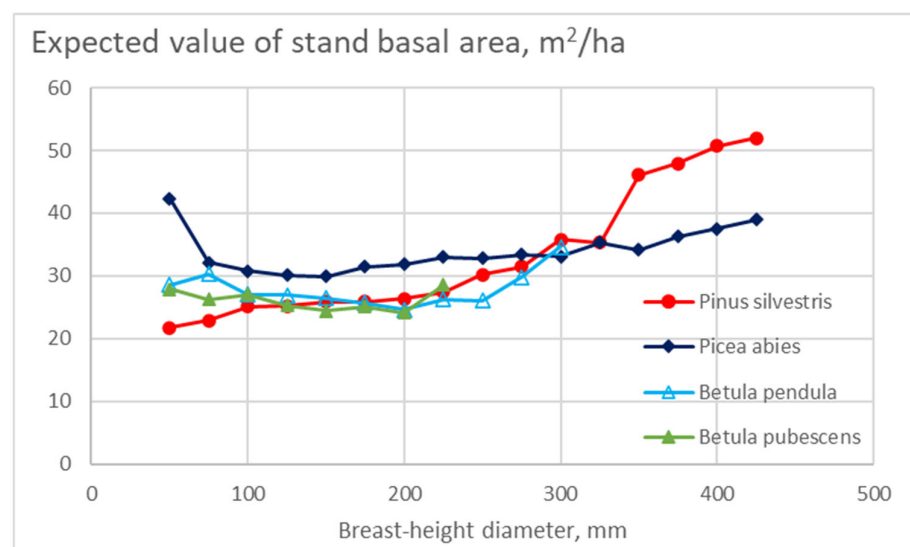


Figure 5. Expected value of stand basal area in different diameter classes for the four tree species.

3.2. Survival Probability Model Results

As the annual mortality rates were produced in Figure 4 according to Equation (3), the alternative technique based on Equation (5) remains to be examined. The results are

shown in Figure 6. It appears that the general level of mortalities agrees with Figure 4, as well as the order between tree species, and most of the within-tree-species trends found in Figure 4.

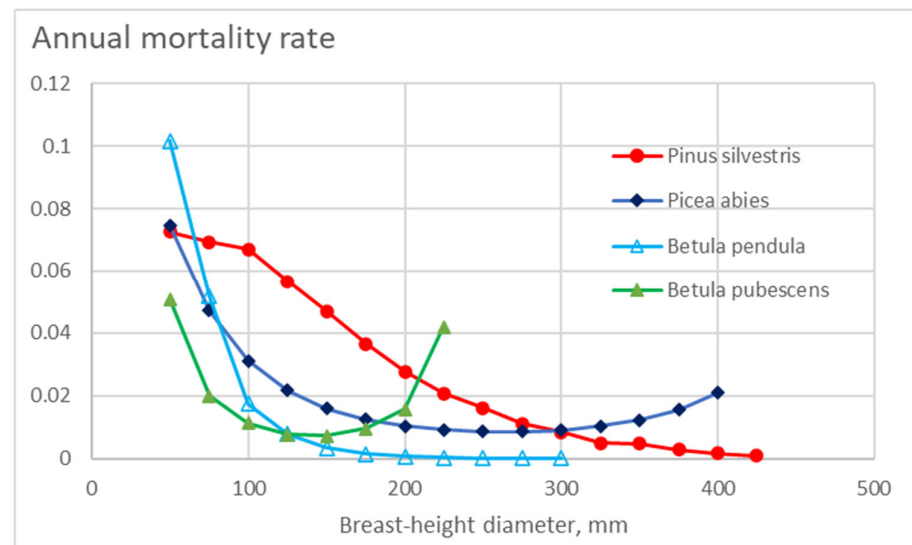


Figure 6. Annual mortality rate in different diameter classes for the four tree species, within a model with three independent variables, where the stand basal area is included as a mean-field approximation, according to Equation (5).

As Equation (5) allows the determination of the annual survival probability as a single function for any tree species, regardless of the duration of the observation periods, the coefficients of such species-specific functions (4) are worth reporting as experimental results. The coefficients are shown in Table 4.

Table 4. Coefficients of Equation (4) applied in Figure 6.

Survival Model [Equation (4)] Parameters					
Tree species		<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula pendula</i>	<i>Betula pubescens</i>
Explanatory variable		1	2	3	4
Constant	a_0	3.489919	1.297552	2.724741	1.341536
D	a_1	-2.92×10^{-5}	0.025801	0.038834	0.06468
D ²	a_2	3.28×10^{-5}	-4.9×10^{-5}	-3.04×10^{-5}	-0.00023
BAL	a_3	-0.046928	0.001631	-0.084363	-0.038454

3.3. Stand-Level Results

As the figures above report the mortality probability of individual trees, the loss rate of basal area, commercial tree volume, or value are of interest from the economic viewpoint. Figure 7 shows the species-specific stand-level relative basal area loss rate for the four tree species as a function of the stand basal area. Interestingly, only the downy birch displays a clear effect of stand basal area on the BA loss rate due to mortality.

Figure 8 shows the species-specific stand-level relative basal area loss rate for the four tree species as a function of the species basal area. All four tree species show a tendency of small minority populations dying out. Interestingly, downy birch again differs from the other tree species by showing a reduced basal area loss rate at larger basal areas of the species.

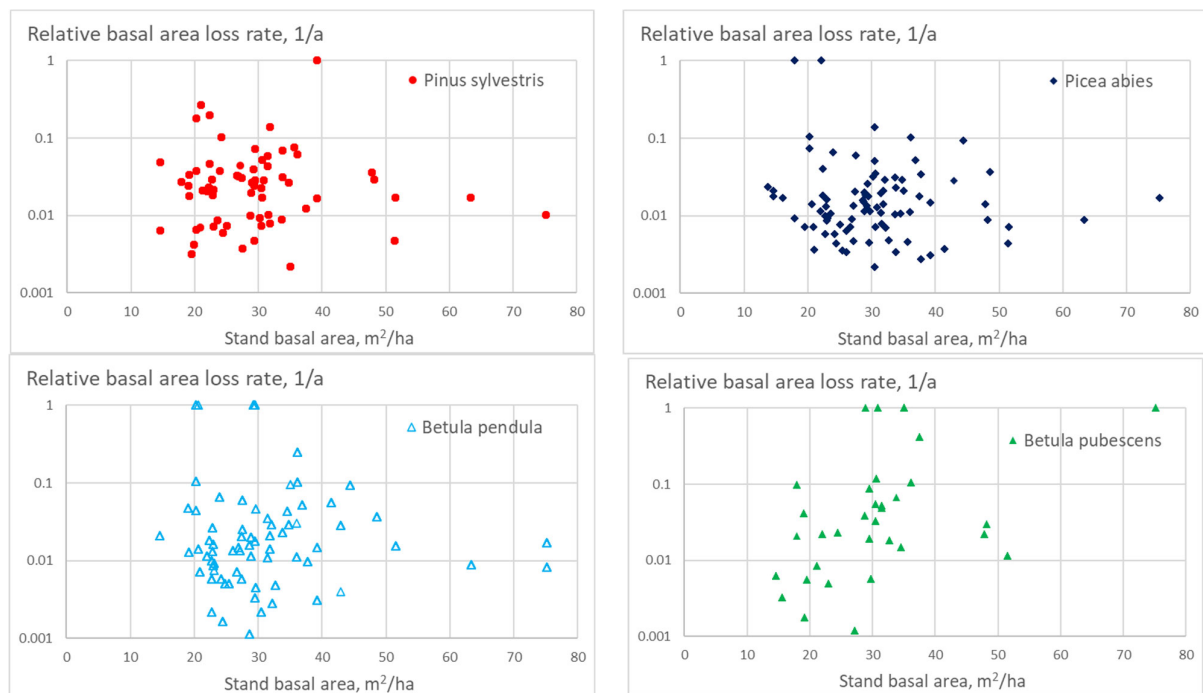


Figure 7. Relative basal area loss rate for four tree species, as a function of the stand basal area.

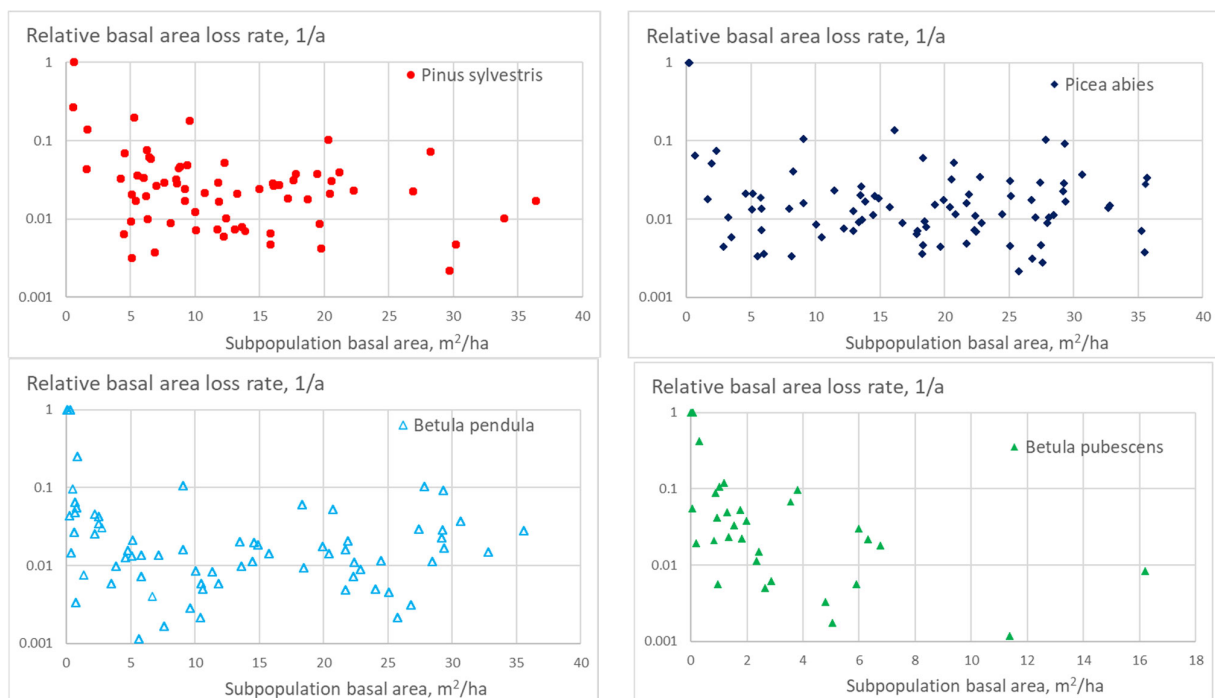


Figure 8. Relative basal area loss rate for four tree species, as a function of the species basal area.

Figure 9 shows the species-specific stand-level relative basal area loss rate for the four tree species as a function of the species basal area in relation to the stand basal area. All four tree species again show the tendency of small minority populations dying out. Downy birch again differs from the other tree species by showing a reduced basal area loss rate at larger relative basal areas of the species.

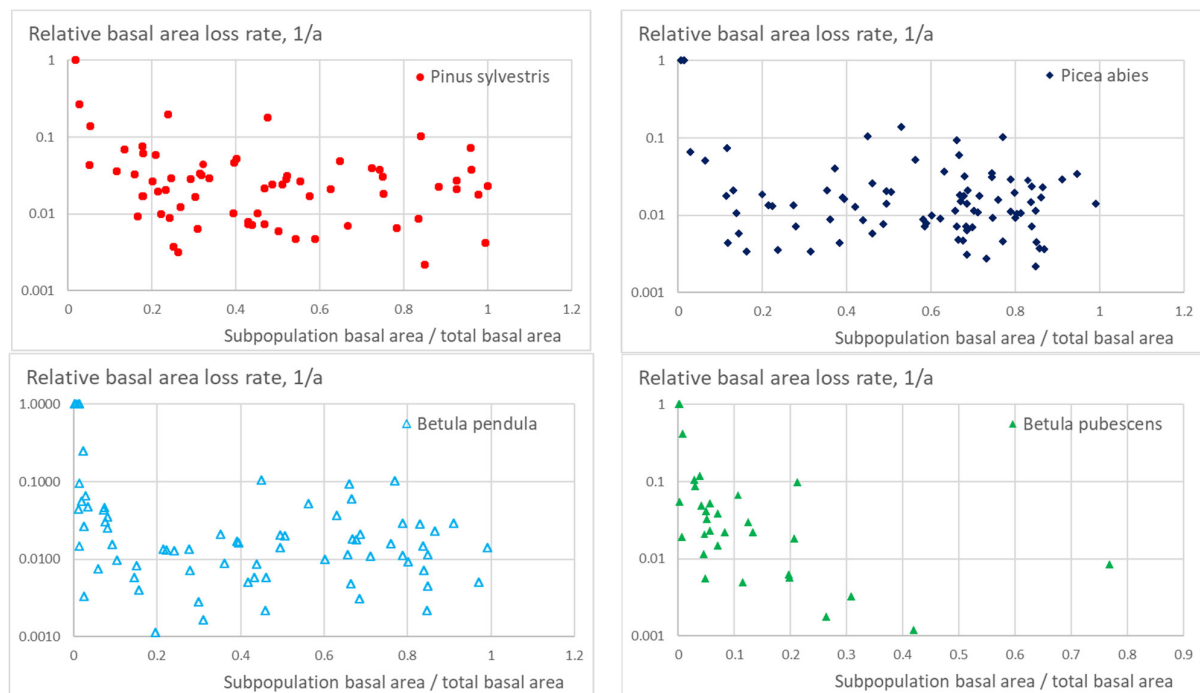


Figure 9. Relative basal area loss rate for four tree species, as a function of species basal area in relation to stand basal area.

Figure 10 shows the species-specific stand-level relative basal area loss rate for the four tree species as a function of stand age. The mortality of Scots pine appears insensitive to stand age. All four tree species again show the tendency of small minority populations dying out. The mortality of Norway spruce and silver birch appears to increase with age after 100 years. Downy birch mortality increases with stand age in the vicinity of 50 years.

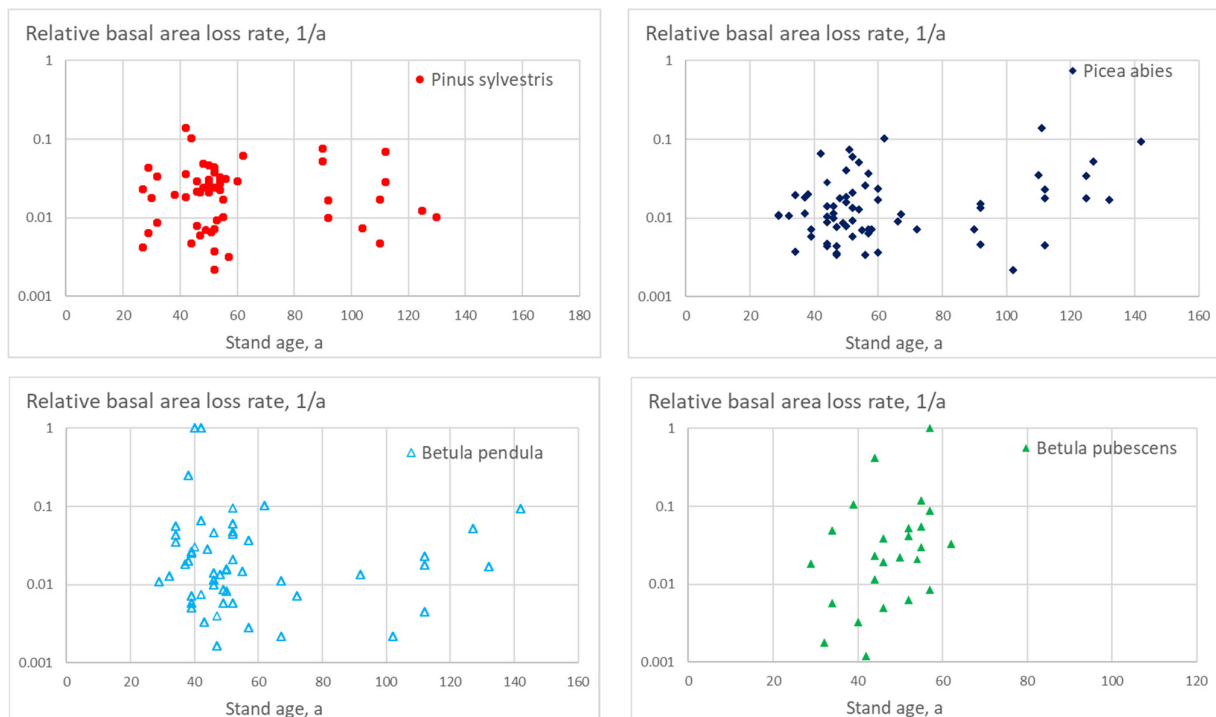


Figure 10. Relative basal area loss rate for four tree species, as a function of stand age.

4. Discussion

A rather interesting observation from Figure 7 is that the basal area loss rate is insensitive to the stand basal area. A consequence is that the mortality of trees does not strongly regulate thinning practices—eventual thinnings can be designed based on other objectives but to prevent trees from dying.

Some studies have indicated mortality to increase along with basal area [43]. The effect of stand basal area on mortality, however, may depend on other mortality drivers as drought, wind, snow, etc. Thinning tends to accelerate wind damage [25]. In the present material, one driver for mortality was 2009–2010 snow damage. The basal area does not necessarily accelerate snow damage, in terms of relative basal area loss [26,44–46]. Apparently, snow damage probability is dominated by abiotic factors, rather than forest stand parameters [25,47,48], but the tree species differ [26,44,49–51].

As the gross mortality over the observation periods appeared from 6% to 12%, the level of annual mortalities in Figure 4 appears to correspond reasonably. Such mortality, however, can be compared to the outcome of models resulting from earlier investigations. The mortality model of Bollandsås [52], parametrized for the present dataset, is shown in Figure 11. It is found that the level of annual mortalities predicted is in the order of one-third, in comparison to Figure 4. In other words, the range of mortalities in Figure 11 runs up to 3% per annum, whereas the range in Figure 4 runs up to 9% per annum. Such a difference appears even if the expected values of the stand basal areas shown in Figure 5 are used in the model parametrization (Figure 11).

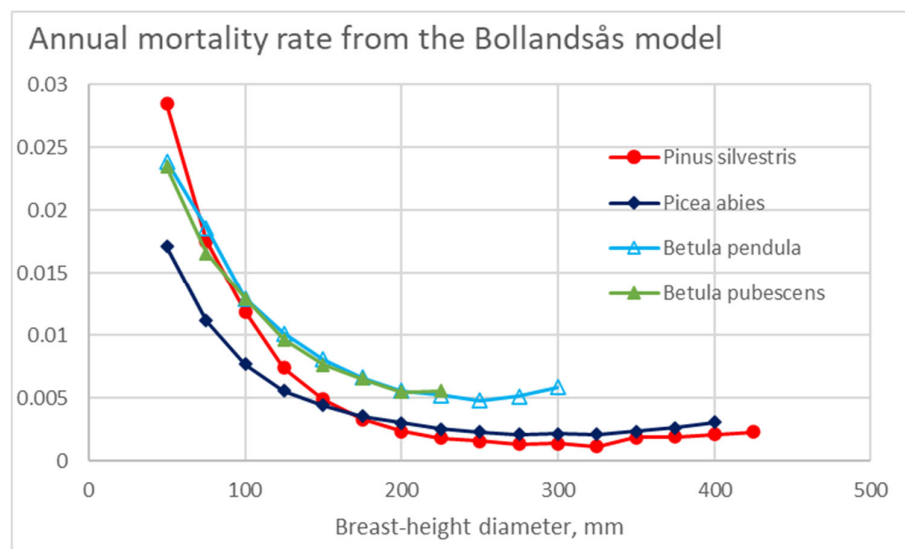


Figure 11. Annual mortality rate in different diameter classes for the four tree species, plotted from the model of Bollandsås [52], parametrized for the present dataset.

The actual reasons for the large difference between the models are unknown. There may be some physical differences inducing the difference in the mortalities. One possible reason for the difference could have been snow damage during the winter 2009–2010, to some degree contributing to all observation periods of the present study. Alternatively, some modeling bias may exist. The expected value of the basal area in the data of Bollandsås has been much lower than in the present material—the model might be unable to represent the binomial mortality effect of the greater level of basal areas.

Another interesting difference is that in Figure 11, the mortalities of birch species are greater than that of conifers. An opposite result is found in Figure 4. The following explanation is hypothesized. Figure 5 shows the expected values of stand basal areas at the beginning of any observation period; birch trees may have experienced a high mortality before any period of observation. Then, during any observation period, the

remaining birch trees may have had a greater rate of survival. Another possible reason for the comparatively low mortality of deciduous trees is the occurrence of snow damage during leafless wintertime [53–55].

The mortality model of Eid and Tuhus [42], parametrized for the present dataset, is shown in Figure 12. It is found that the level of annual mortalities predicted is in the same magnitude as in the Bollandsås model (Figure 11), i.e., the order of one-third in comparison to Figure 4. However, in the case of three of the four tree species, the annual mortality is less dependent on tree diameter than in the case of the Bollandsås model (Figure 11). It is not known to which degree the differences between Figures 11 and 12 are due to different datasets and to which degree to modeling techniques [42,56].

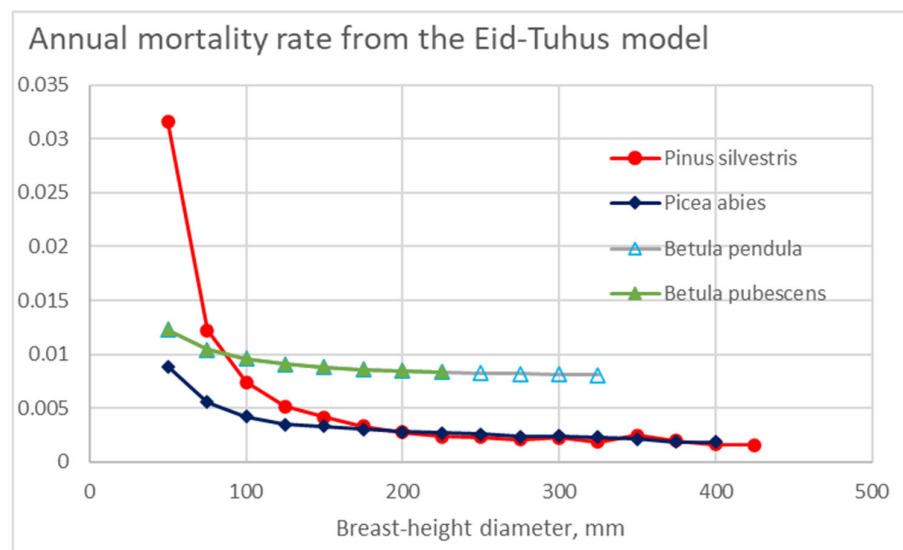


Figure 12. Annual mortality rate in different diameter classes for the four tree species, plotted from the model of Eid and Tuhus [42], parametrized for the present dataset.

A variety of mortality investigations have been published with non-boreal tree species or with datasets from different climatic and ecological regions. Models resulting from such investigations are not necessarily transferable to the present dataset, but the magnitude of the mortality results can be compared.

The magnitude of mortalities in Germany and Switzerland, reported by Hülsmann et al. [15,57], appear to comply with the magnitudes of Figures 11 and 12, rather than Figures 4 and 6, in the case of *Pinus* and *Picea* species, whereas mortalities reported by Etzold et al. were higher [40]. A similar magnitude of mortality has been reported in the Eastern and Central United States [58]. In the case of *Betula* species, there is a closer compliance to Figures 4 and 6. Mortalities in hemi-boreal Estonian forests, as well as a variety of other European forests, have also had closer correspondence to Figures 11 and 12 [23,59]. European fully stocked Beech and Pine forests have shown mortalities at least on the level of Figures 4 and 6 [60]. Boreal tree species in Belarus [9], with stocking densities comparable to the present dataset, also have corresponded to mortalities on the level of Figures 4 and 6.

The annual mortality in old-growth forests of the Pacific Northwest has been reported [30,61] in the vicinity of or below one percentage, in closer correspondence to Figures 11 and 12 than to Figures 4 and 6. Similar levels have been observed in the Sierra Nevada mountains [62]. Even smaller mortalities have been observed in Southern Pine ecosystems [63]. Some observations, however, have recently indicated increasing mortality [31]. In Eastern North America, conifers affected by spruce budworm defoliation have observed mortality rates closer to those in Figures 4 and 6 [64].

Average annual mortality rates between 1% and 2% have been reported for East African arid woodlands [65].

Interestingly, some qualitative patterns appearing in Figures 4 and 6 can be compared with the literature. In the case of young trees, the mortality of Scots pine is greater than that of Norway spruce, whereas in the case of old trees, the relationship is the opposite [23]. The mortality of downy birch in Figure 4 and 6 appears to be a non-monotonic function of tree size that positively corresponds to observations with a few short-lived tree species [23,66].

As Figures 8 and 9 indicate, small minority species within stands tend to die out; this finding agrees with sparse literature observations [38].

As the mortality observed in this dataset is much higher than in earlier studies in Nordic countries, potential explanations are needed. The 2009–2010 snow damage was mentioned. Is there possibly some identifiable phenomenon behind the observed snow damage? The fact is that winter precipitation has been increased as one manifestation of changing climate, and further increments are predicted for the future [67,68]. As conifers are more susceptible to snow damage [26,44,51], deciduous trees can be favored to mitigate the problem. On the other hand, stand-replacing damage can be avoided by enhanced timber stock retained in thinnings.

5. Conclusions

The mortality rate of boreal trees was found to be the order of three times that predicted by earlier Nordic mortality models, being in the upper range of international literature observations. Small subpopulations of any tree species tend to die out. The mortality of downy birch increases with stand basal area, as well as with stand age. The mortality of Norway spruce and silver birch increases after 100 years, while that of Scots pine is invariant to age. It is suspected that the high mortality of conifers is due to climatic phenomena of anthropogenic origin. As the relative loss rate of basal area is insensitive to the stand basal area, the mortality of trees does not strongly regulate thinning practices, but stand-replacing damage can be avoided by retaining a larger timber stock, along with an enhanced proportion of deciduous trees.

Funding: This study was partially financed by Niemi Foundation.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are contained within the article.

Acknowledgments: Ilkka Korpela and Aarne Hovi contributed to the data collection.

Conflicts of Interest: The author declares no conflict of interest.

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