Predicting decay and ground vegetation development in *Picea abies* snag stands

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Abstract

In a *Picea abies* (L.) Karst. (Norway spruce) mountain forest on the Gandberg site in the northern Swiss Alps, trees were killed by bark beetles in 1992–1997. A combination of field studies and dynamic modelling was used to project snag decay and future ground vegetation succession in these steep, unharvested stands. In permanent plots, ground vegetation cover and natural tree regeneration have been monitored annually since 1994. To obtain additional information on the abundance of snags, logs, boulders and other microsite types in these stands, the relative frequency of the microsite types was quantified along four strip transects on the montane and subalpine elevational levels. A dynamic model of snag decay and ground vegetation development was constructed (modified matrix model approach). Based on field data and literature values, the model was parameterised and initialised separately for the montane and the subalpine level. For model validation, microsite types were quantified in 2001 with the line-intercept method on both elevational levels. Starting from the conditions in the stands before the bark beetle attacks, it was possible to project short-term succession and to accurately simulate the decay and ground vegetation patterns eight years after tree die-back. Long-term simulations suggest that on the montane level, raspberries (*Rubus idaeus* L.) will be replaced by *Picea abies*, while on the subalpine level ferns will dominate for a long time.

Introduction

Insect infestations are a common disturbance factor in forest ecosystems (Holsten 1990; Parminter and Daigle 1997; Forster 2001). They can alter competitive relationships between plants not only directly through selective mortality, but also indirectly because defoliation triggers a carbon and nutrient release (Beudert 1999). Hence, insect infestations can alter the successional pathways in forests (Fleming 2000). Several short-term developmental patterns were reported after strong (>80%) beetle-caused tree mortality in various

forest stands: (1) fast and extensive invasion by *Rubus idaeus* L. (raspberries, cf. Batzer and Popp 1985; Crawford et al. 1993; Osawa 1994; Hogget 2000), (2) slight to massive spread of *Calamagrostis villosa* (Chaix) Gmelin or *C. canadensis* (Michx.) Beauv. (reed grasses, cf. Yeager and Riordan 1953; Reif and Przybilla 1995; Schulz 1996; Holsten and Burnside 1997; Cole et al. 1999; Wurz and Wahrenbrock 2000; Heurich 2001; Jehl 2001), (3) invasion of *Rubus fruticosus aggr*. L. (blackberries) and other species that are characteristic of clear-cuts (Märkl and Eglseer 2001), and (4) a quick development of pioneer tree stands dominated by

Alnus (alder, cf. Matsuoka et al. 2001) and *Betula* (e.g., *B. papyrifera* var., paper birch, cf. Baker and Kemperman 1974).

In a *Picea abies* (L.) Karst. (Norway spruce) mountain forest on the Gandberg in the northern Swiss Pre-Alps, trees were killed by *Ips typographus* L. (European spruce bark beetle) at the montane and subalpine elevational levels between 1992 and 1997 (Forster 1993; Wermelinger et al. 1999; Walcher and Kupferschmid 2001). Subsequently, the ground vegetation at the montane level changed into a *Rubus idaeus* association (Kupferschmid 2002), while at the subalpine level *Calamagrostis villosa* dominated together with ferns (mainly *Dryopteris dilatata*, *D. filix-mas*, *Oreopteris limbosperma* and *Athyrium filix-femina*) and mosses (e.g., *Polytrichum formosum*, *Hylocomium splendes*, *Thuidium tamariscinum*) (Kupferschmid 2001). Thus, the two elevational levels on the Gandberg site represent two of the most frequent short-term developmental patterns after beetle-caused conifer tree die-back (see 1–2 above).

Both *Rubus idaeus* and *Calamagrostis*-fern communities are known to provide few favourable microsites for tree establishment (e.g., Leibundgut 1984; Lieffers et al. 1993; Walker 1994), and thus they tend to slow down the succession towards tree-dominated communities. In a steep mountain forest such as the Gandberg snag stands, it is important to know how long a *Rubus idaeus* or *Calamagrostis*-fern dominance will last, because neither *Rubus* brushwood nor *Calamagrostis* carpets nor fern tussocks provide effective protection against snow avalanches and rockfall, whereas *Picea abies* mitigates natural hazards that may cause damage to people or assets (Brang et al. 2001). In this article, we present a quantitative model to project succession in mountain snag stands.

In many current forest succession models, ground vegetation is disregarded, and the focus is entirely on trees (e.g., Botkin et al. 1972; Horn 1975; Monserud and Sterba 1996; Golser and Hasenauer 1997; Hasenauer et al. 2000; Huth and Ditzer 2000; Bugmann 2001). However, tree regeneration is often competing heavily with ground vegetation, especially when *Rubus*, *Calamagrostis* or ferns dominate (cf. Sims and Mueller-Dombois 1968; Walker 1994; Wurz and Wahrenbrock 2000; Heurich 2001). Therefore, we propose that a model for our purpose needs to combine the dynamics of ground vegetation with those of tree regeneration.

Kellomäki and Väisänen (1991) included in their tree succession model SIMA three types of ground vegetation: 'pioneer', 'intermediate' and 'climax' species groups. *Picea abies* seedlings and saplings were part of the climax group. Their distribution was dependent on light and nutrients, and the parameters were assumed to be the same as for mature spruce trees. However, no shading or direct influences of ground vegetation species on *Picea* regeneration were considered. In our snag stand, tree regeneration may not be limited primarily by light availability (which depends on canopy structure) or nutrients, but it may rather depend on local soil structure and the growth form of the competing ground vegetation species. A simplification of all these complex processes is to merge all the abiotic and biotic influences on a specific small area (typically $< 1 \text{ m}^2$) by defining microsite types based on soil structure (e.g., deep soil, boulders) and the dominant species of the ground layer (e.g., *Polytrichum*, *Rubus*, etc.). Microsite types can easily be recognised in field sampling. Tree regeneration can then be modelled separately on each microsite, with microsite-specific rates of tree germination, growth and mortality.

To take into account the changes in the ground vegetation or the transitions between the microsite types, respectively, we first derived a succession model for the ground vegetation. At the core of this succession model is a Markov approach, distinguishing transition probabilities from each microsite type into all other microsite types. In those cases where the transitions do not depend on how the forest reached its present state but only on the present state itself, and when the transition probabilities are constant over time, the matrix approach was found to be both powerful and convenient (cf. Waggoner and Stephens 1970; Van Hulst 1979). With such a first-order Markov chain approach, other authors have successfully simulated changes between landscape types (e.g., Cherrill et al. 1995), vegetation zone types (e.g., Starfield and Chapin 1996), forest structure types (e.g., Bebi et al. 2001), species (e.g., Enright and Ogden 1979) and the states of decay of 'woody' microsites such as snags, logs, etc. (e.g., Raphael and Morrison 1987; Kruys et al. 2002). Nevertheless, to our knowledge this approach has never

been used for modelling changes of herbaceous microsite types.

Therefore, the objectives of the present paper were as follows:

1. to classify the ground vegetation patterns at the Gandberg site into microsite types that are amenable to an analysis of successional processes;
2. to use this information to develop and test a dynamic model of the decay and ground vegetation succession for a period of 8 years (1993–2001);
3. to predict the future successional pathways of the Gandberg forest on the montane (dominated by *Rubus*) and subalpine (dominated by *Calamagrostis* and ferns) level.

Below, we present the field sampling methods that were used to estimate model parameters and to obtain an independent data set for model validation. We then describe the model structure, model initialisation and parameterisation as well as a first set of simulation results. In a second step, which is beyond the scope of the present paper, an additional module will be added to this model, where tree germination, growth and mortality are modelled separately for all microsite types (cf. RegSnag model by Kupferschmid et al., submitted for publication).

Study site

The study site is located on the north face of the Gandstock, south of Schwanden (canton of Glarus, Switzerland) at an elevation of 1100–1600 m a.s.l. The Gandberg inclines towards the North at an angle of about 18–36° (40–80%), and the site does not receive direct sunshine between October and April as a result of orographic shading. The soil is an acid brown soil with a tendency to podsol (Roth 1996). Its depth varies greatly due to the presence of red conglomeratic Verrucano (cf. Oberholzer and Heim 1900–1908) boulders deposited by rockfall, mainly at the montane level. Precipitation and temperature are not recorded directly on the Gandberg site, but nearby in Glarus and Linthal/Tierfehd. The estimated mean annual precipitation for the Gandberg forest is 1600–2000 mm and the mean annual temperature 2–3 °C (Kupferschmid Albisetti 2003).

Before the *Picea* die-back, which started in 1992, the entire Gandberg forest was dominated by *Picea abies* (L.) Karst. (Norway spruce). Only a few *Abies alba* Miller (silver fir, 1%) and *Acer pseudoplatanus* L. (sycamore maple, 3%) trees were present. The stands belong to the *Galio-Abieti-Piceetum* association at the montane level and to the *Homogyno-Piceetum vaccinietosum myrtilli* association at the subalpine level. The stands at the montane level developed after a clear-cut in 1842–1846, and were later subject to some thinning (Forstverwaltung Kt. Glarus 1949). The stands at the subalpine level have always been more open and probably subject to little thinning only (Forstverwaltung Kt. Glarus 1949). In 1990, the forest had a growing stock of about 820 m³/ha at the montane level and 590 m³/ha at the subalpine level (Kupferschmid Albisetti et al. 2003).

Between 1992 and 1997, a large outbreak of *Ips typographus*, triggered by the windstorm event 'Vivian' in 1990, caused the death of almost all *Picea abies* trees in an area of approximately 100 ha, with a mortality peak in 1993, when about 20 ha of *Picea abies*-dominated stands died on the Gandberg site alone (Walcher and Kupferschmid 2001). Only about 2% of the *Picea* trees, but all *Abies alba* and *Acer pseudoplatanus* trees survived, scattered throughout the snag stands.

Field data for model initialisation and parameterisation

Permanent plots

Since 1994, ground vegetation succession and tree regeneration have been investigated in a pilot study on 24 permanent plots of 1 m × 1 m at the lower montane level of the Gandberg site, where *Picea abies* trees had died in 1993 (Kupferschmid 2002, Kupferschmid et al. 2002). The cover of plants and mosses with a frequency larger than 5% was estimated annually (cf. Figure 5 and Kupferschmid 2002).

In 2001, the frequency of 25 different microsite types was estimated additionally in these permanent plots (Figure 1). These microsite types had been defined for the entire Gandberg forest (cf. Table 1) according to (i) the dominant plant and moss species and the associated soil surface characteristics (i.e. boulders, raw humus, mull), or
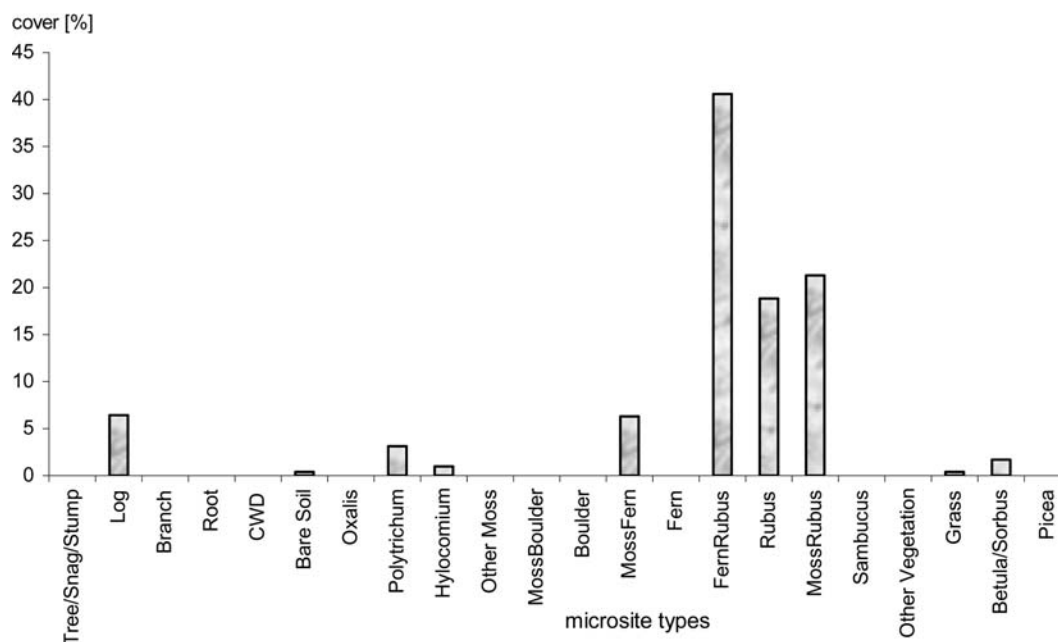
Figure 1. Frequency of the 25 microsite types (defined in Table 1) in the permanent plots of the lower montane level of the Gandberg site in 2001. Some microsite types have frequencies of zero due to the location of the plots, i.e. they were not represented in the permanent plots (e.g., snags, stumps or boulders).

(ii) the decomposition stage of woody debris (see 'strip transects', below).

Strip transects

To complement the permanent plot data, which covered only 24 m², the frequency of microsite types was also quantified by a spatially more extensive sample along four strip transects that were placed parallel to the contour lines (simply called 'transects' below) in summer 2000. Two transects with a length of 100–160 m and a width of 5 m were placed in two former *Galio-Abieti-Piceetum* associations (lower montane level at 1280 m and upper montane level at 1360 m a.s.l.) and in two *Homogyno-Piceetum vaccinietosum myrtilli* associations (lower subalpine level at 1520 m and upper subalpine level at 1570 m). Along these transects, plots of 5 m × 5 m were delineated and the percent cover of 13 common microsite types was estimated per plot (cf. Figure 2). On the basis of this first classification of microsite types, a more detailed classification (i.e. 25 types) was derived and used in 2001 in the permanent plots (see above and Table 1). In addition, the diameter and length of all logs and snags in the transects were measured and the timber volume of the snag stands was calculated (cf. Kupferschmid Albisetti et al. 2003).

Nomenclature

The nomenclature of Lauber and Wagner (1996) was used for ground vegetation and tree species; Oberdorfer (1993) for herbaceous plant associations; Ott et al. (1997) for forest associations.

Model description

General model description

A modified matrix model approach (for a description of classic matrix models see e.g., Vanclay 1994; Caswell 2001) was used to study the temporal development of the frequency of microsite types at the montane and subalpine levels of the Gandberg site. The model does not track the location of the microsites (i.e. it is spatially non-explicit), and it operates with an annual time step. A schematic diagram of the model is given in Figure 3.

Table 1. Estimated microsite type frequencies for the years 1993 and 2001 on the entire montane and subalpine level.

Microsite types			Estimated cover (%)			
Names	Definition	Abbreviation	Montane		Subalpine	
			1993	2001	1993	2001
Tree	Living overstory tree, mostly *Picea abies*	Tre	1.0	0.0	1.0	0.0
Snag	Dead, but standing tree	Sna	0.0	0.5	0.0	0.5
Stump	Rest of broken snag = stump	Stu	0.0	0.4	0.0	0.4
Branch	Accumulations of branches and bark pieces	Bra	0.0	2.0	0.0	2.0
Log	Tree lying on the surface = log	Log	0.0	3.6	0.0	3.6
Root	Roots of trees, snags and stumps not yet rotten	Roo	4.0	2.3	4.0	2.3
CWD	Coarse woody debris = rotten stumps, logs, etc.	CWD	1.0	3.0	1.0	3.0
Bare soil	Bare soil, raw humus, needles	Soi	51.0	0.6	64.0	7.0
Oxalis	Dominated by *Oxalis acetosella*	Oxa	20.0	0.4	1.7	1.0
Polytrichum	Dominated by *P. formosum* or *P. alpinum* cushion	Pol	5.0	5.7	1.0	30.0
Hylocomium	Dominated by *H. splendes* or *Thuidium tamariscinum*	Hyl	1.0	1.5	0.1	0.2
Moss	Dominated by other mosses; montane level: mostly liverworts, subalpine level: mostly *Sphagnum* cf. *quinquefarion*	Mos	1.5	0.4	0.1	2.0
MossBoulder	Mosses that cover boulders (but not dens 'Pol' or 'Hyl')	MoB	4.0	4.5	2.0	2.2
Boulder	Read conglomeratic stones and boulders	Bou	9.0	8.0	5.0	4.0
MossFern	Mosses under ferns	MoF	0.0	6.5	0.7	14.0
Fern	Dominated mostly by *Dryopteris dilatata*, *D. filix-mas*, but also *Orepteris limbosperma* and *Athyrium filix-femina*	Fer	0.0	3.0	3.0	14.0
FernRubus	Fern under *Rubus idaeus*	FeR	0.0	27.5	0.1	0.5
Rubus	Dominated by *Rubus idaeus*	Rub	0.0	11.0	0.1	0.3
MossRubus	Mosses under *Rubus idaeus*	MoR	0.0	14.0	0.1	0.5
Sambucus	Dominated by *Sambucus racemosa*	Sam	0.0	0.2	0.6	0.6
Other vegetation	other herbs: montane level: mostly *Senecio ovatus*, *Galium ovatum* subalpine level: mostly *Vaccinium myrtillus*	Veg	2.5	4.0	5.5	2.6
Grass	Dominated mostly by *Calamagrostis villosa*, but also *Carex sp.* and *Avenella flexuosa*	Gra	0.0	0.5	10.0	8.5
Betula	Dominated by newly established *Betula pendula* regeneration >1.3 m	Bet	0.0	0.2		
Sorbus	Dominated by newly established *Sorbus aucuparia* regeneration >1.3 m	Sor	0.0	0.1	0.0	0.4
Picea	Dominated by newly established *Picea abies* regeneration >1.3 m	Pic	0.0	0.2	0.0	0.4
All			100.0	100.0	100.0	100.0

Data sets for the montane level are based on the permanent plots (cf. Figures 1 and 5) and the strip transects (cf. Figure 2), the ones for the subalpine level only on the strip transects (cf. Figure 2). The estimations for the year 1993 were used as initialisation data in the model, those of 2001 for model verification. Short definitions and abbreviations of each microsite type are included (altered after Kupferschmid Albisetti 2003).

The model consists of two sub-models; one for the microsite types with woody material ('Logs', 'Branches', etc.), and one for all non-woody microsite types, including 'Boulders', 'Bare soil' and all types with plant cover (cf. Figure 3). This splitting was necessary because of the peculiarities of the 'woody' microsite types, particularly with respect to dead trees, as described below.

Woody microsite types: During the tree decay process, the area occupied by a living tree stem changes into 'Snag' area and then into 'Stump' area, with no associated change in area. However, during this decay process additional woody microsites are created, such as 'Branches' and

'Logs' (Figure 4). These new woody microsites cover areas formerly occupied by non-woody microsite types. New logs are created when a snag breaks, and the area occupied by new logs was assumed to be a multiple of that of the snag area (cf. Figure 4; 'area correction factors' explained in section 'Model parameterisation'). Correspondingly, the area covered by new logs was assumed to reduce the area of the non-woody microsite types in proportion to their occurrence in the simulation. In a similar manner, additional area was created for the microsite type 'Branches' during the decay process of standing dead trees. Obviously, these transitions cannot be implemented using a standard matrix model approach.
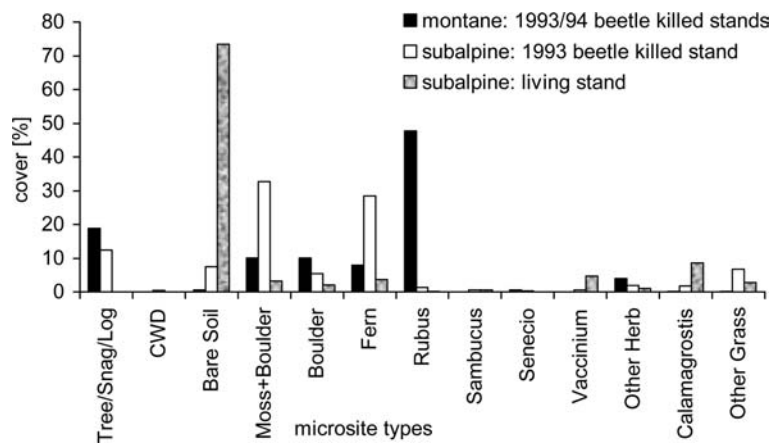
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Figure 2. Frequency of the 13 most common microsite types in the strip transects in 2000. Black bars: mean cover in stands at the lower montane elevational level, where trees died in 1993, and in stands at the upper montane level, where trees died in 1994. White bars: mean cover of stands at the upper subalpine level, where trees died in 1993. Grey bars: mean cover in still living stands at the upper subalpine level.
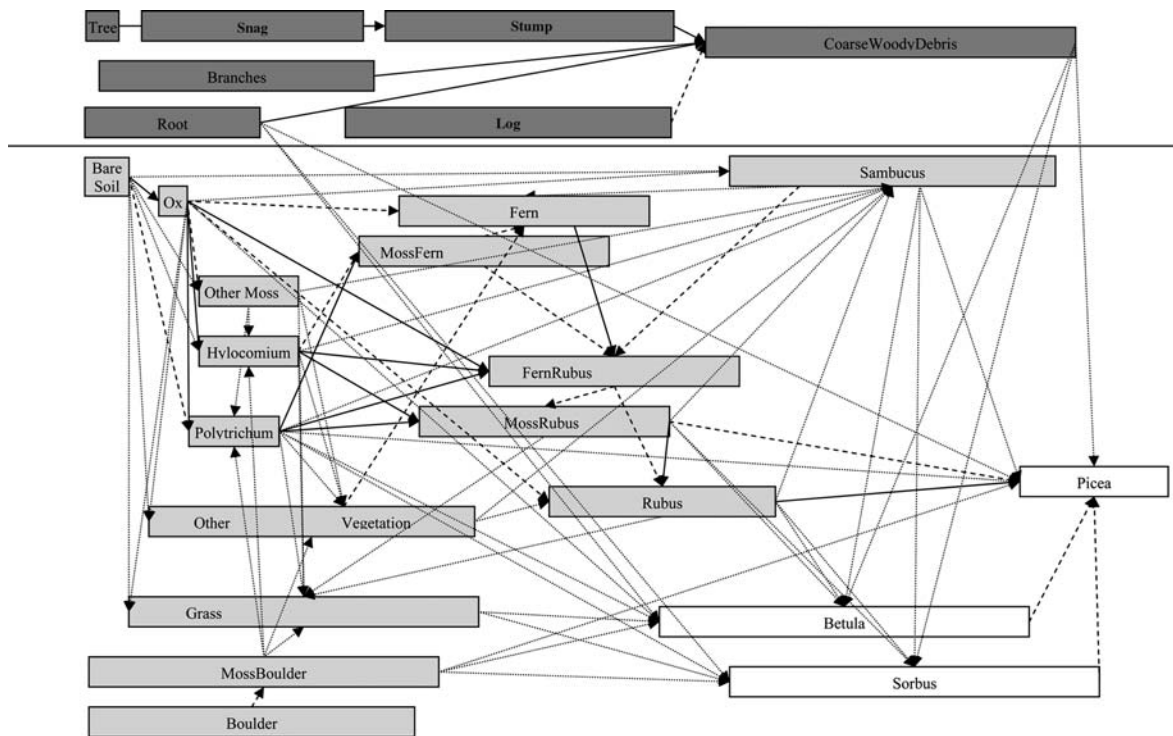

Figure 3. Schematic diagram of the simulation model. The boxes represent the 25 microsite types included in the model. Dark grey boxes are woody microsite types, light grey boxes are types dominated by stones, bare soil or ground vegetation, and white boxes are types dominated by trees. For the montane elevational level all transitions between microsite types are shown with arrows: thick arrows denote frequent transitions (annual probability >5%), dashed arrows less frequent transitions (1–5%) and dotted arrows rare transitions (<1%). Note that no arrows are drawn from non-woody microsite types to 'Logs' or 'Branches'. The width of the boxes represents differences in the residence times of the various microsite types (except in the case of Picea).
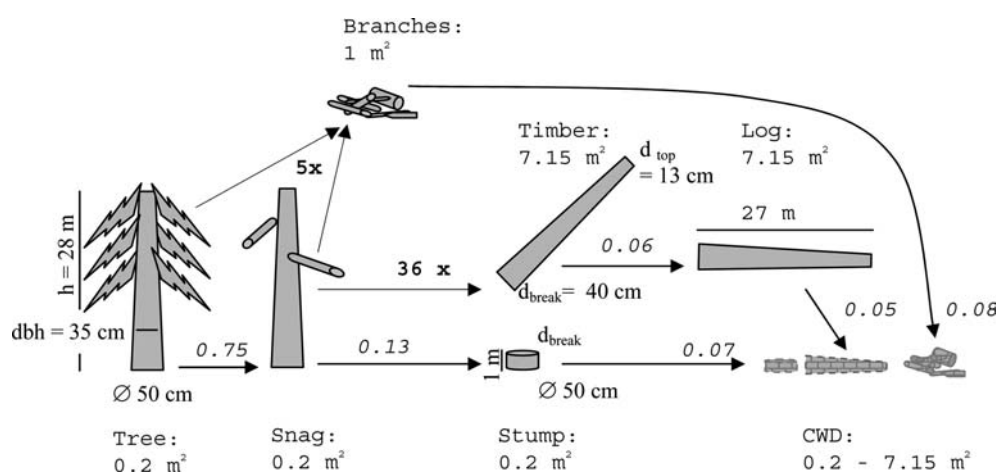
Figure 4. Decay of a dead tree: sketch of the area occupied by different woody microsite types (defined in Table 1) at the soil surface. Italicised are transition probabilities between these woody microsite types and for the microsite types 'Branches' and 'Timber'/'Logs' the area correction factor applied in the model is shown (for calculation, see text). The width of the tree, snag, and stump is enlarged in the picture.

Non-woody microsite types: All the other changes between microsite types were assumed to conform to the standard matrix model approach, and thus were calculated using transition probabilities. The fundamental assumptions of this approach are that (1) the rates of change depend only on the current state and not on previous (historical) states (i.e. first order Markov model) and (2) there is a finite number of microsite types (in our case, a total of 25 types, cf. Table 1).

In the following sections, the derivation of the initial values and parameters is explained. For the non-woody microsite types, two sets of initial values and parameters were estimated; one for the entire montane elevational level (1200–1400 m a.s.l.) and one for the subalpine level (1520–1600 m). This division seemed appropriate due to the different structures of the forest stands (different forest associations) and the different ground vegetation cover before and after tree die-back (cf. Figure 2 and section 'Introduction').

Model initialisation

The model was used to simulate an area of 100 m², and it was initialised with the conditions inferred for the Norway spruce stands in 1993 (cf. Table 1). At that time, *Picea* trees had already been attacked by bark beetles but still contained their needles, and therefore it is reasonable to assume that the

ground vegetation was still similar to that in a living stand.

Woody microsite types (montane and subalpine stands)
In the transects, 513–560 living trees and snags per ha were observed in 2000, with an average diameter at breast height of 35 cm, a projected diameter at the soil surface of 50 cm and an average height of living or dead unbroken trees of 28 m (cf. Figure 4) at all elevational levels (Kupferschmid Albisetti et al. 2003). For the microsite type 'Tree', we therefore assumed that 5 trees were present per 100 m², each of them covering a basal area of about 0.2 m² at the soil surface (cf. Figure 4), resulting in a cover of 1% for the microsite type 'Tree' (cf. Table 1). Furthermore, we assumed that no snags and no fresh stumps (microsite type 'Stump') were present in 1993 (cf. Table 1), but only rotten stumps and rotten logs (microsite type 'Coarse Woody Debris', called 'CWD' below).

In 2000, 68 rotten stumps ha^{-1} were present at the montane level, and 10 rotten stumps ha^{-1} at the subalpine level (Kupferschmid Albisetti et al. 2003). In the subalpine transects, the rotten stumps together with the rotten logs covered an area of about 1% (Figure 2). At the montane level, the frequency of the microsite type 'CWD' was estimated as zero because most rotten logs and also most decaying stumps were covered by *Rubus idaeus* (Figure 2). However, because the montane

level had been managed more heavily than the subalpine level, we expected fewer logs (but more stumps) on the montane level, and therefore 1% was judged to be a good estimate also for the abundance of the microsite type 'CWD' on the montane Gandberg for the year 1993 (cf. Table 1). We assumed that very few branches were present on the forest floor in 1993, and hence we set the initial frequency of the microsite type 'Branches' to zero (cf. Table 1).

Finally, an estimate of the microsite type 'Root' had to be calculated. *Picea abies* trees on the Gandberg are characterised by large amounts of roots at the soil surface or on boulders. We assumed that the microsite type 'Root' occupies 0.8 m^2 per tree, thus resulting in a total of 4% 'Root' cover for the 5 trees/100 m^2 (cf. Table 1).

Non-woody microsite types on the montane level
The non-woody microsite types include all other microsite types present on the Gandberg forest such as 'Boulders', 'Bare Soil' and all types with plant cover. Almost no quantitative information was available on the frequency of these microsite

types prior to tree death. The only data available were from three 1 m × 1 m ground vegetation cover assessments carried out by Kägi (1992) and from the 24 permanent plots since summer 1994 (Figure 5, Kupferschmid 2002). The following strategy was used to derive the initialisation values for the year 1993 (cf. Table 1): (1) from the comparison of the data of Kägi (1992) with the permanent plot data in 1994, it seemed likely that only the cover of *Oxalis acetosella* had increased considerably between tree death and spring 1994, as a consequence of tree defoliation; (2) the permanent plots were quite small, and hence they neither included snags nor large boulders. Therefore, the transect data recorded in the year 2000 (cf. Figure 2) were used to estimate the microsite types 'Boulder' and 'MossBoulder' (i.e. Moss + Boulder in Figure 2 minus the mosses in Figure 5).

Non-woody microsite types on the subalpine level
In contrast to the montane level, the initialisation values of the subalpine level (cf. Table 1) were estimated from the cover of the microsite types underneath groups of living *Picea abies* trees in
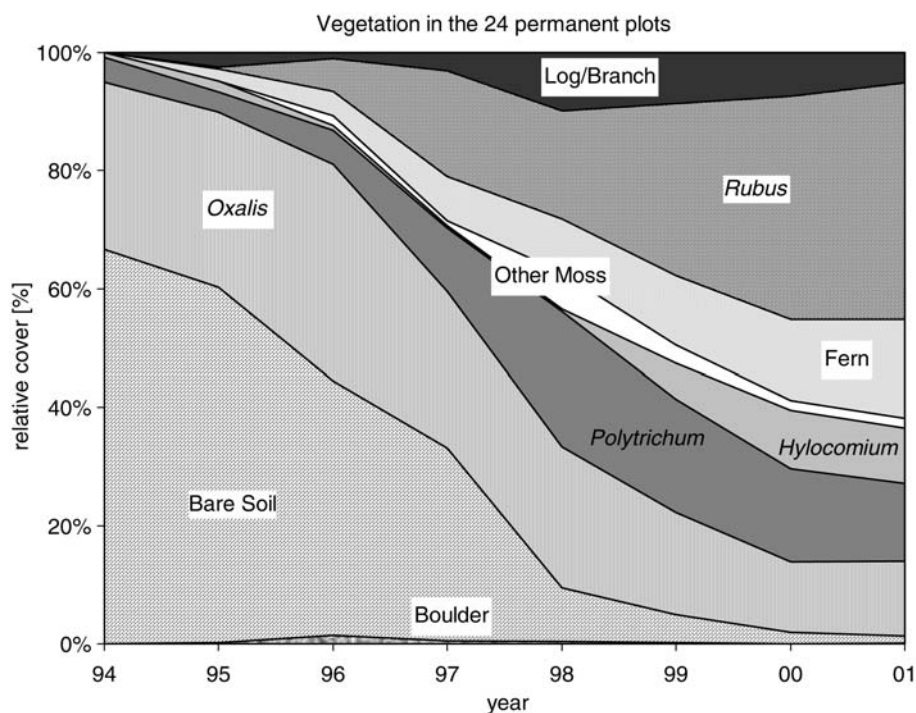

Figure 5. Succession observed in the permanent plots on the Gandberg site. Only the cover of the most frequent plants, boulders, bare soil and logs was used here to calculate total cover, which exceeded 200%. Note that these are not microsite types, but percentage of areas covered with a plant in percent of total cover (sum of all these percentages). Modified after Kupferschmid (2002).

2000 in the transects at the upper subalpine level (living stands, Figure 2). There, *Polytrichum formosum* and *P. alpinum* were far more abundant than all the other mosses (Kupferschmid 2001). We therefore assigned almost all (i.e. 98%) moss microsite types to the microsite type 'Polytrichum' (cf. Table 1).

Model parameterisation

Transition probabilities involving woody microsite types (cf. Figure 4)

Tree–Snag. After the lethal bark beetle infestation, trees lost their needles during the first year (i.e. defoliation) and the fine brushwood until the end of the second year. In the literature, a time lag of at least 2–3 years was reported for *Picea* until woody decomposition started, i.e. until mass loss occurred (e.g., Harmon et al. 1986, Shorohova and Shorohova 2001; Tarasov and Birdsey 2001). For our model, a time lag of 3 years was assumed, i.e. 98.5% of the dead trees were assumed to have lost their needles and fine brushwood after 3 years. Using an exponential decay curve, this results in a transition probability from the microsite type 'Tree' to 'Snag' of about 0.75 yr^{-1} (i.e. $1 - (\text{tree}_{t\,=\,3}/\text{tree}_0)^{1/t} = 1 - (1.5/100)^{1/3} \cong 0.75 \text{ yr}^{-1}$ cf. Figure 4).

Snag–Stump. In the strip transects, about 25% of the trees were broken below 10 m above the ground in the year 2000, and 50% of the trees were broken close to the tree top or at least higher than 10 m (Kupferschmid Albisetti et al. 2003). Classifying only the former as 'broken' and the latter as '1/3 broken', 42% of the snags had changed to stumps in the 4 years between the end of the time lag (see above) and the year 2000. The decay rate from the microsite type 'Snag' to 'Stump' was therefore calculated (again assuming an exponential decay curve) as a constant of 0.13 yr^{-1} (cf. Figure 4). This is well within the range of decay rates reported by Harmon et al. (1986).

Stump–CWD (coarse woody debris), Log–CWD, Branch–CWD and Root–CWD. According to the literature, the decay rate of *Picea abies* logs is between 0.016 and 0.05 yr^{-1} (Shorohova and Shorohova 2001; Tarasov and Birdsey 2001). Smaller diameter classes tend to decay faster than larger ones (Tarasov 1999). As conditions on the north-facing Gandberg are likely to be more humid than those in Russia, we estimated the decay rate for the microsite type 'Stumps' and 'Roots' into 'CWD' to be 0.07 yr^{-1}, for 'Logs' 0.05 yr^{-1}, and for 'Branches' 0.08 yr^{-1}.

Snags–Timber and non-woody microsites–Logs. In the model, an artificial state 'Timber' was defined to allow for a better simulation of the decay process from snags via 'hanging' logs (= 'Timber') to the microsite type 'logs on the soil surface' (= 'Logs', cf. Figure 4). When snags become stumps, 'Timber' is produced with the same probability, but the ground area occupied by 'Timber' is larger than that occupied by a snag, which is a consequence of the length of the logs. We assumed that on average, snags were 28 m tall (cf. section 'Initialisation') and had a point of breakage at 1 m above the forest floor (note that a snag may break several times before it finally breaks at this low height), resulting in a timber length (l_{timber}) of 27 m and a diameter at the break point (d_{break}) of 0.4 m (interpolated between the diameter at soil surface (0.5 m) and the dbh (0.35 m), cf. Figure 4). For the lying logs in the transects, we measured a diameter loss of 1 cm per 1 m of tree height (Kupferschmid Albisetti et al. 2003). Hence, according to Eq. (1) a log occupies an area (a) of approximately 7.15 m^2.

$$
\begin{aligned}
a &= l_{\text{timber}} * \frac{d_{\text{break}} + d_{\text{top}}}{2} \\
&= l_{\text{timber}} * \frac{d_{\text{break}} + (d_{\text{break}} - (l_{\text{timber}} * 0.1))}{2}
\end{aligned}
\tag{1}
$$

$$
a = 27 * \frac{0.40 + (0.40 - (27 * 0.1))}{2} = 7.5 \,\text{m}^2
$$

Consequently, this area, which is created when the transition from a snag to a stump occurs, is about 36 times larger than that of 'Snags' (0.2 m^2), resulting in an area correction factor of 36 (cf. Figure 4).

In the permanent plots, hanging logs (i.e. our state 'Timber') first occurred in winter 1996/1997 (Kupferschmid 2002). In 2001, 25% of the logs lay directly on the ground, resulting in 6.5% areal cover by the microsite type 'Logs' (cf. Figure 1 in contrast to Figure 2, where timber, snags and stumps are merged, resulting in 12 and 19% total cover of woody microsite types on the montane and subalpine levels). The transition probability from 'Timber' to 'Logs' was therefore calculated as 0.06 yr^{-1}.

The area newly covered by logs was assumed to reduce the cover of the microsite types 'Roots', 'CWD' and all non-woody microsite types (except for the microsite types 'Picea', 'Sorbus' and 'Betula') in proportion to their occurrence at a given time step.

Effects of branches on the frequency of non-woody microsite types. We assumed that both 'Trees' and 'Snags' lost branches, and that in the year 2001 about 50% of the branches had fallen already (Kupferschmid, pers. obs.). As with logs, it was not 'Tree' and 'Snag' microsite types that changed into the microsite type 'Branches', but other non-woody microsite types were covered by fallen branches, and obviously this area was larger than the area of the 'Trees' and 'Snags' from which the branches originated. To take this into account, an area correction factor for the generation of branch microsites was estimated. Branches and fine brushwood were found to amount to about 8–13% of the merchantable timber mass (Dauber and Kreuzer 1979; Kramer and Krüger 1981) and about 10% of the total timber volume (Kaufmann 2001), respectively. With an average timber volume per tree of about 1 m^3 (average dbh = 35 cm, and using the local timber tariff of Schwanden), this led to 0.5 m^3 of branches for the 5 trees per 100 m^2. With an average diameter of the branches of about 5 cm, 10 m^2 would be covered by branches from 5 trees. However, we assumed that about 50% of the branches would lie on top of other branches, thus resulting in a maximum of about 5 m^2 of the microsite type 'Branches' from these 5 trees. The 5 trees together covered 1 m^2, therefore the area correction factor for the surface area covered by branches was 5 (cf. Figure 4). We assumed that branches were mostly found below the former tree crowns. The area newly covered by branches was therefore assumed to reduce the area of the microsite types 'Bare Soil' and 'Oxalis', and only to a lower extent (1/3) also the area of the microsite types 'Polytrichum', 'Hylocomium' and 'Other Mosses', always in proportion to their occurrence at a given time step.

CWD–Picea, CWD–Betula and CWD–Sorbus. *Picea abies* height growth is fairly slow on coarse woody debris (Eichrodt 1969; Newsome et al. 1995), and seed years are infrequent at this elevation (Mencuccini et al. 1995), so that new recruitment cannot occur every year. Furthermore, *Betula pendula* and *Sorbus aucuparia* regeneration

was even less frequent on the Gandberg site than *Picea* regeneration (Kupferschmid et al. 2002). We therefore assumed a very small transition probability from 'CWD' to the microsite type 'Picea' (0.005 yr^{-1}) and an extremely small one to 'Betula' and 'Sorbus' (0.001 yr^{-1}).

Root-Picea, Root-Betula and Root-Sorbus. Only *Picea abies* was assumed to be successful in establishing on roots. The transition probability from 'Root' to 'Picea' thus was set to an extremely small value (0.001 yr^{-1}).

Transition probabilities of non-woody microsite types at the montane level (cf. Table 2)
We primarily used the ground vegetation development observed in the permanent plots from 1994 to 2001 (Figure 5, Kupferschmid 2002) to parameterise the matrix model. The estimates of the transition probabilities (Table 2) were derived in three steps.

First step. The microsite type distributions in 1993 and in 2001 (cf. Table 1) were derived based on the proportions of microsite types in the permanent plots (Figures 1 and 5) and in transects at the montane and upper montane elevational level (Figure 2).

Second step. We made assumptions about the self-replacement probabilities of all microsite types based on the observed succession in the permanent plots (Table 1 and Figure 5) and additional information from a literature survey. The self-replacement probabilities (p_{self}) were calculated for each microsite type using Eq. (2) (cf. Caswell 2001).

$$p_{self} = 1 - (1/resTime), \qquad (2)$$

where resTime is the residence time of a microsite type, i.e. the mean lifetime of this microsite type. As logs and branches normally fall onto non-woody microsites, the residence times of these non-woody microsite types were smaller than they would have been without the falling logs and branches. The effective self-replacement probabilities (p_{self_eff}) in the matrix sub-model (which is considered here separately from the decay sub-model) are therefore the sum of the p_{self} calculated from the residence times (upper values in the diagonal of the matrix in Table 2) and the transitions into 'Logs' and 'Branches' (lower values in the diagonal of the matrix in Table 2). These transitions are calculated in the decay sub-model

Table 2. Transition matrix for the montane elevational level with all transition probabilities between non-woody microsite types.

Microsites	Soi	Oxa	Pol	Hyl	Mos	MoB	Bou	MoF	Fer	FeR	Rub	MoR	Sam	Veg	Gra	Bet	Sor	Pic
Soi	0.333 + 0.130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxa	0.5	0.252 + 0.130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pol	0.02	0.42	0.545 + 0.065	0	0.005	0.005	0	0	0	0	0	0	0	0	0	0	0	0
Hyl	0.005	0.06	0	0.598 + 0.065	0.005	0.001	0	0	0	0	0	0	0	0	0	0	0	0
Mos	0.005	0.02	0	0	0.598 + 0.065	0	0	0	0	0	0	0	0	0	0	0	0	0
MoB	0	0	0	0	0	0.959 + 0.03	0.02	0	0	0	0	0	0	0	0	0	0	0
Bou	0	0	0	0	0	0	0.95 + 0.03	0	0	0	0	0	0	0	0	0	0	0
MoF	0	0	0.06	0.05	0.15	0	0	0.9 + 0.03	0	0	0	0	0	0	0	0	0	0
Fer	0	0.02	0	0	0	0	0	0.05	0.9 + 0.03	0	0	0	0.005	0.01	0	0	0	0
FeR	0	0.07	0.2	0.2	0.09	0	0	0.02	0.07	0.9 + 0.03	0	0	0.01	0	0	0	0	0
Rub	0	0.02	0	0	0	0	0	0	0	0.05	0.876 + 0.03	0.06	0	0.005	0	0	0	0
MoR	0	0	0.12	0.08	0.08	0	0	0	0	0.02	0	0.896 + 0.03	0	0	0	0	0	0
Sam	0.001	0.001	0.001	0.001	0.001	0	0	0	0	0	0.001	0.001	0.952 + 0.03	0.005	0	0	0	0
Veg	0.005	0.005	0.005	0.005	0.005	0.001	0	0	0	0	0	0	0	0.95 + 0.03	0	0	0	0
Gra	0.001	0.001	0.001	0.001	0.001	0.001	0	0	0	0	0.001	0.001	0	0	0.96 + 0.03	0	0	0
Bet	0	0.001	0.001	0	0	0.001	0	0	0	0	0.001	0.001	0.001	0	0.005	0.97	0	0
Sor	0	0	0.001	0	0	0.001	0	0	0	0	0.001	0.001	0.001	0	0.005	0	0.97	0
Pic	0	0	0.001	0	0	0.001	0	0	0	0	0.09	0.01	0.001	0	0	0.03	0.03	1

Definitions and abbreviations of the microsite types are listed in Table 1. Self-replacement transition probabilities (upper values) and the temporary constant transitions into the microsites 'Logs' and 'Branches' (lower values) are listed in the diagonal of the matrix, even though they have not been implemented in the model built on the software Stella. For the estimation of the transition probabilities, we refer to the text and Kupferschmid Albisetti (2003).

(cf. section 'Parameterisation involving woody microsite types'), and they clearly vary over time. As in a standard matrix only constant parameters can be used, the transitions into the microsite types 'Logs' and 'Branches' were temporarily held constant during the estimation of all other transition probabilities. The transitions into the microsite type 'Logs' were set to 0.03 and into 'Branches' to 0.1 (for 'Bare Soil' and 'Oxalis') and 0.035 (for 'Polytrichum', 'Hylocomium' and 'Other Mosses'), respectively (lower value in the diagonal in the matrix in Table 2).

The residence times (resTime) could often be estimated from the mean time a plant dominated or was frequent in the permanent plots (Figure 5, Kupferschmid 2002). In Kupferschmid Albisetti (2003), the derivation of every single residence time is explained in detail.

Third step. We made additional assumptions regarding the possible transitions between all the non-woody microsite types based on the ground vegetation succession in the permanent plots (Table 1 and Figure 5) and data from the literature. The following set of assumptions was used to estimate these transition probabilities (cf. Table 2):

– In a transition matrix, the column total must always equal 1, therefore the sum of all the transition probabilities from one specific microsite type into all *other* microsite types (p_{other}) is constrained by

$$p_{\text{other}} = \sum p_{ij} = 1 - p_{\text{self\_eff}}, \qquad (3)$$

where p_{ij} denotes the transition between all non-woody microsite types (*i* and *j*) (cf. Table 2).
– Succession is assumed to always move forward and not backward. For example, 'Bare Soil' cannot arise out of 'Rubus', 'Fern' or the other microsite types into which it changed in early succession; similarly, the mosses lost underneath *Rubus idaeus* cannot regrow.
– Large values of transition probabilities were estimated to an accuracy of 1%; very small transition probabilities were assumed to be 0.005 yr^{-1}, and extremely small transition probabilities were assumed to amount to 0.001 yr^{-1}.

In Kupferschmid Albisetti (2003), the derivation of every single transition probability is explained in detail.

Transition probabilities of non-woody microsite types at the subalpine level (cf. Table 3)

A procedure similar to the one for the montane level was used. However, we primarily used the data from the strip transect at the upper subalpine level (Figure 2), because no data from permanent plots were available for the subalpine level. Again, the derivation of every single transition probability is explained in detail in Kupferschmid Albisetti (2003), and the final values are shown in Table 3.

Validation data

In spring 2001, the percent cover of the same 25 microsite types as in the permanent plots (cf. Table 1) was estimated using the line-intercept method in Norway spruce stands in which *Picea* trees had died in 1993 (for a description of the method see e.g., Canfield 1941; Parker and Savage 1944). Sampling took place at four elevational levels (lower montane: 1220–1280 m a.s.l., upper montane: 1310–1370 m, lower subalpine: 1460–1520 m, upper subalpine: 1540–1600 m). At each of the four elevational levels, eight groups of lines were selected randomly. Each group contained four lines 10 m long which were parallel ('E–W'), perpendicular ('N–S') and at an angle of 45° to the contour lines ('N–W', 'N–E'). Along these 128 lines (four elevational levels × 8 groups × 4 lines per group), the length of each microsite type was measured with a measuring tape. From the lengths measured, the frequency of each microsite type was calculated. The set of four lines at each location was chosen so as to minimise errors due to vertically and horizontally different dimensions of the various microsite types.

As the frequencies of all microsite types were very similar on the montane elevations (Kupferschmid and Bugmann 2005), we evaluated the model simulations against a validation data set that comprised the entire montane level. In contrast, the validation data of the lower subalpine level represent the ground vegetation of a transition zone between montane and subalpine vegetation (see e.g., Figure 6, cf. Kupferschmid and Bugmann 2005). We therefore evaluated the model separately against the data from the lower subalpine and the upper subalpine level (see section Results, Figure 6, Table 4).

Table 3. Transition matrix for the subalpine elevational level. The structure of the table is identical to that of Table 2.

| Microsites	Soi	Oxa	Pol	Hyl	Mos	MoB	Bou	MoF	Fer	FeR	Rub	MoR	Sam	Veg	Gra	Bet	Sor	Pic
Soi	0.618 + 0.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxa	0	0.801 + 0.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pol	0.2	0.04	0.852 + 0.065	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Hyl	0.001	0	0	0.872 + 0.065	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mos	0.005	0	0	0	0.9 + 0.065	0	0	0	0	0	0	0	0	0	0	0	0	0
MoB	0	0	0	0	0	0.958 + 0.03	0.02	0	0	0	0	0	0	0	0	0	0	0
Bou	0	0	0	0	0	0	0.95 + 0.03	0	0	0	0	0	0	0	0	0	0	0
MoF	0	0	0.07	0.06	0	0	0	0.929 + 0.03	0	0	0	0	0	0.05	0	0	0	0
Fer	0.035	0.02	0	0	0	0	0	0.04	0.969 + 0.03	0	0	0	0	0.04	0	0	0	0
FeR	0.001	0.001	0.001	0.001	0	0	0	0.001	0.001	0.965 + 0.03	0.005	0.001	0	0	0	0	0	0
Rub	0	0.001	0	0	0	0	0	0	0	0	0.96 + 0.03	0	0	0	0	0	0	0
MoR	0	0	0	0	0	0	0	0	0	0	0	0.967 + 0.03	0	0	0	0	0	0
Sam	0.001	0.001	0	0	0	0	0	0	0	0.005	0.005	0.001	0.95 + 0.03	0	0	0	0	0
Veg	0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0.878 + 0.03	0	0	0	0
Gra	0.005	0.005	0.005	0.001	0.035	0	0	0	0	0	0	0.001	0	0	0.969 + 0.03	0	0	0
Bet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sor	0.001	0	0.001	0	0	0.001	0	0	0	0	0	0	0.005	0.001	0.001	0	0.97	0
Pic	0.001	0	0.005	0	0	0.001	0	0	0	0	0	0	0.005	0.001	0	0	0.03	1
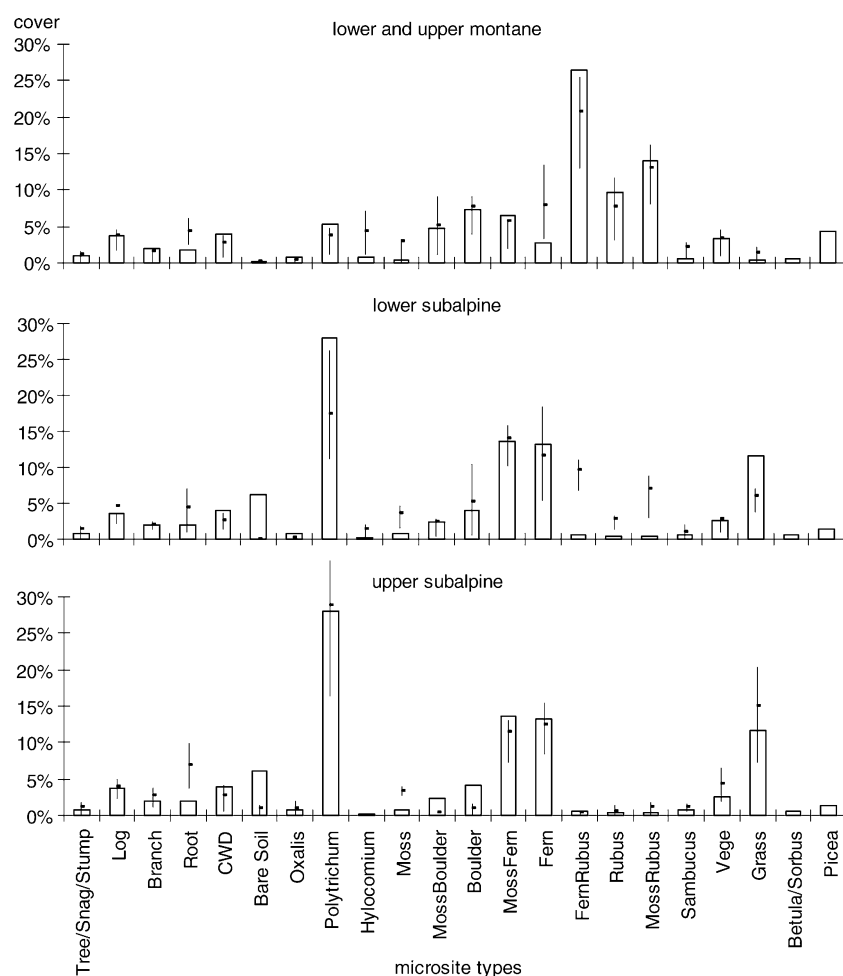
Figure 6. Model validation: simulated microsite type frequencies after 8 simulation years (white bars) performed with the montane and subalpine initialisation and parameterisation set, respectively. Observed microsite type frequencies in 2001 (validation sampling) are represented by vertical lines, where the ends of these lines are the 25%- and 75%-quartiles and the points the mean values at the entire montane level ($n = 16 \times 4$ lines), the lower subalpine level (transition zone, $n = 8 \times 4$ lines) and the upper subalpine level ($n = 8 \times 4$ lines) of the Gandberg site.

Model implementation and simulation experiments

The model was implemented with the software STELLA (a software for model-building and simulation, High Performance Systems 2001), using array structures for the 'matrix' part of the model. Therefore, in contrary to a 'real' matrix, no self-replacement was modelled explicitly. For the integration, Euler's method (cf. High Performance Systems 2001) was used with a time step of one year (discrete time model).

Firstly, simulations were performed over 8 years (1993–2001) with both sets of initial values and parameters, i.e. with the transition matrices parameterised for the montane (cf. Table 2) and subalpine (cf. Table 3) levels. These simulations enable (i) a verification of the model (comparison with data from the permanent plots from 1994 to 2001 and data from strip transects in 2000) and (ii) a validation of the model (comparison with the independent data from 2001 that were sampled for model validation).

Secondly, long-term (i.e. 25 years) simulations were performed (i) to test the model behaviour in the long run (i.e. sensitivity analysis) and (ii) to evaluate the future succession of the montane and subalpine stands on the Gandberg site.

Table 4. Similarity index (s_i) for each microsite type i on the entire montane, and both subalpine elevational levels according to Eq. 4 (see text for details).

| | Similarity index | | |
| | Montane | Subalpine | |
	Mean	Lower	Upper
Tree/Snag/Stump	0.8	0.7	0.8
Log	1.0	0.9	1.0
Branch	0.9	1.0	0.9
Root	0.6	0.6	0.4
CWD	0.8	0.8	0.8
Bare Soil	0.7	0.0	0.3
Oxalis	0.7	0.4	0.9
Polytrichum	0.8	0.8	1.0
Hylocomium	0.3	0.2	0.4
Moss	0.2	0.4	0.4
MossBoulder	1.0	1.0	0.3
Boulder	1.0	0.9	0.4
MossFern	0.9	1.0	0.9
Fern	0.5	0.9	1.0
FernRubus	0.9	0.1	0.8
Rubus	0.9	0.2	0.7
MossRubus	1.0	0.1	0.4
Sambucus	0.4	0.8	0.7
Other Vegetation	1.0	1.0	0.7
Grass	0.5	0.7	0.9
Betula/Sorbus	0.0	0.0	0.0
Picea	0.0	0.0	0.0
Total 22 microsites	0.7	0.6	0.6

Note that the ground vegetation on the lower subalpine level of the Gandberg site represented a transition between the montane and upper subalpine vegetation.

Simulation results

Montane level

Comparison with estimated microsite frequencies (model verification)

First, we compared the simulated microsite frequencies after 8 simulation years with the estimated microsite frequencies for the year 2001. The latter data were based on the frequencies in the permanent plots and the strip transects in the year 2001 (cf. Table 1). Note that this is not a validation of the model, but a check whether the estimated parameters yield the simulation result we desired, and therefore it is a check of the plausibility of the estimated transition probabilities for the Gandberg site.

On the montane level, the simulated microsite frequencies (white bars in Figure 6) corresponded quite well with the estimated microsite frequencies (Table 1). Only the amount of the microsite type 'Picea' was overestimated strongly in the model (but see sensitivity analysis).

Comparison with independent field data (model validation)

In a next step, we compared the simulated frequencies after 8 simulation years with the microsite frequencies sampled along lines in 2001 on the two montane levels of the Gandberg site (validation data set). An index of similarity (s) was calculated using Eq. (4), similar to Bugmann (1994) and Badeck et al. (2001):

$$s = \frac{\sum_{i=1}^{22}(s_i)}{22}, \quad \text{where } s_i$$
$$= 1 - \left(\frac{|\text{ validation}_i - \text{simulation}_i|}{\text{validation}_i + \text{simulation}_i} \right), \quad (4)$$

where i stands for the 25 microsite types ('Tree', 'Snag' and 'Stump' were lumped and so were 'Sorbus' and 'Betula'). The similarity index can take values between 0 and 1, where 1 corresponds to a total agreement between the simulation and the validation data. Results are shown in Table 4.

The distribution of microsite types was quite similar after 8 years of simulation (white bars in Figure 6) compared with the field data in 2001 (points in Figure 6). Overall, the similarity indices s amounted to 0.7 (Table 4). However, with the assumptions we used, the model strongly underestimated the frequency of the microsite types 'Root', 'Hylocomium', 'Other Mosses', 'Fern', 'Sambucus' and 'Grass' ($s_i \leq 0.6$, cf. Figure 6 and Table 4). In contrast, the frequency of the microsite type 'Picea' was overestimated considerably (Figure 6), as it was not found at all on the Gandberg site in 2001. However, it has to be kept in mind that in the microsite type assignment during the validation sampling, moss microsites that contained *Picea* saplings of up to 40 cm in height were still counted as moss microsite types (cf. Table 1). Furthermore, the transition between 'Rubus' and 'Picea' is gradual in nature, i.e. there is a rather long time when both species co-dominate the microsite, whereas in the model this boundary is discrete.

Applying Mann–Whitney U tests separately for each of the 25 microsites, no significant difference could be found between the mean frequency in the
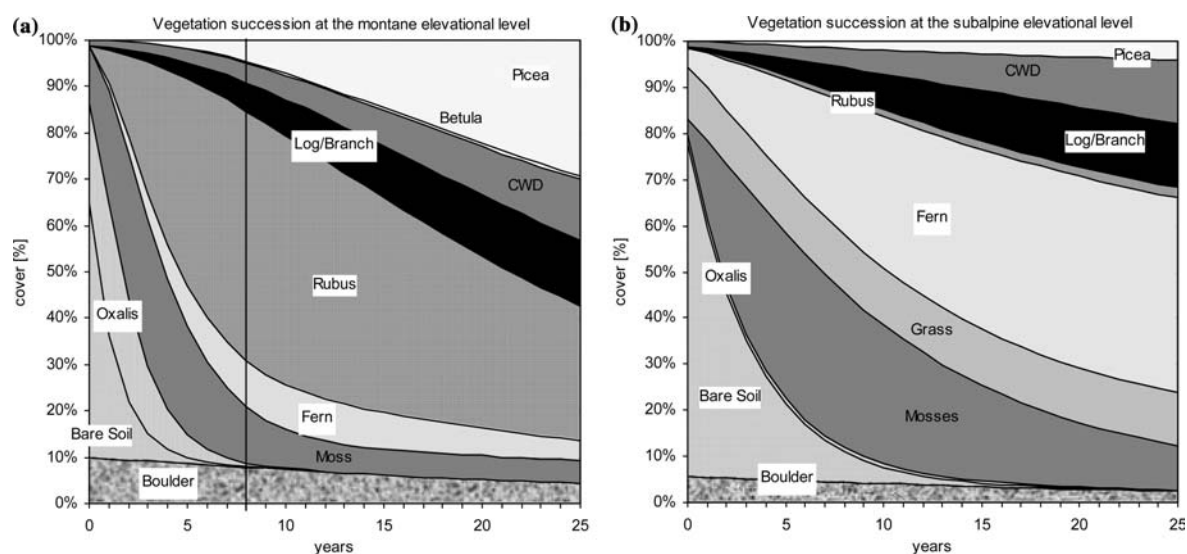
Figure 7. Short-term simulation of the frequencies of the most important microsite types on the montane level (a) and subalpine level (b). Some microsite types were pooled for better comparison of the first 8 years with the results from permanent plots of the Gandberg site (Figure 5) and simpler conclusions for the later years (e.g. Rubus represents 'Rubus', 'MossRubus' and 'FernRubus').

Gandberg in 2001 (16 groups, each representing a mean of 4 lines) and the simulated value 8 years after tree death ($p \geqslant 0.05$).

Subalpine level

Comparison with estimated microsite frequencies (model verification)
The simulated microsite frequencies after 8 simulation years on the subalpine level (Figure 6, white bars) coincide quite well with the estimated microsite frequencies on the upper subalpine level based on the transects (Table 1). Nevertheless, the amount of the microsite type 'Grass' was overestimated and that of 'Polytrichum' underestimated with the model (Figure 6, white bars) compared with the estimates for the subalpine level in 2001 (Table 1, but see sensitivity analysis).

Comparison with independent field data (model validation)
The distribution of microsite types was quite similar after 8 simulation years for the subalpine level compared with the field data sampled along lines in 2001 on the lower and upper subalpine levels (Figure 6, Table 4: $s = 0.6$, $p \geqslant 0.05$ in Mann–Whitney U tests). However, with the assumptions we used, the simulation for the subalpine level considerably ($s_i \leq 0.6$) underestimated the fre-

quency in the microsite types 'Root', 'Hylocomium', 'Other Mosses' and MossRubus. In contrast, the microsite type 'Bare Soil' was overestimated (Figure 6 and Table 4). As we parameterised our subalpine model with data from the transect in the upper subalpine zone, the simulation considerably underestimated the microsite type frequencies of 'FernRubus', 'Rubus' and 'MossRubus' of the transition zone, i.e. the lower subalpine level (Figure 6 and Table 4). On the upper subalpine level, however, the site was less rocky than simulated, resulting in an overestimation of 'Boulder' and 'MossBoulder' in the model compared with the field data (Figure 6 and Table 4).

Time course of succession

Comparison with permanent plot data
For the montane level, we were able to compare the temporal sequence of plant cover in the permanent plots (Figure 5) with those of the microsite type frequencies during the first 8 simulation years (left part of Figure 7a). The abundance of the various microsite types over time was in quite good agreement with the dominance of plants in the Gandberg forest. However, the microsite type 'Rubus' and in particular 'CWD' and 'Picea' emerged too quickly in the simulation (cf. Figure 5 and left part of Figure 7a).

Sensitivity analysis

As mentioned above, the microsite type 'Picea' emerged too quickly and was overestimated in the model using the parameters for the montane level. We therefore decreased the transition probability from the microsite type 'Rubus' into 'Picea' in a stepwise manner from 0.09 yr^{-1} (Table 2) to 0.001 yr^{-1}. As a consequence, after 8 simulation years the frequency of the microsite type 'Rubus' increased from 10 to 13%, while 'Picea' decreased from 4 to 1%. After 25 years, the 99% decrease in the transition probability resulted in a 82% decrease of the frequency of 'Picea' (28% vs. 5% 'Picea' cover). This effect was caused by the higher self-replacement probability of 'Rubus'.

In the model with the parameters for the subalpine level, the microsite 'Grass' was overestimated considerably. We therefore decreased the transition probability from the microsite type 'Polytrichum' into 'Grass' in a stepwise manner from 0.005 yr^{-1} (Table 3) to 0.001 yr^{-1}. This modification caused an increase in the frequency of 'Polytrichum' of 1% and a decrease in 'Grass' of the same amount. Both changes lasted from the 7th simulation year until the end of the simulation (25 years).

These two simple examples of sensitivity analyses show that our model is fairly sensitive to the values of the transition probabilities. However, as the simulation results match well the actual frequencies on the Gandberg site (validation data set), we are confident that the model can be used with the current parameter set for the montane and the subalpine levels to simulate the microsite frequencies of about the first 25 years. It is noteworthy that the steady state of this modified matrix model is equivalent to a 100% dominance of the microsite type 'Picea', which obviously is not realistic and thus limits the temporal domain of model applicability to a few decades.

Simulations over 25 years

Simulation results over longer time periods (25 years) are shown in Figure 7a and b. At the montane level, the various microsite types with raspberry (*Rubus idaeus*) are projected to continue to dominate the ground vegetation in the future (Figure 7a). However, according to the model, *Rubus* will slowly be substituted by a new forest dominated almost exclusively by *Picea abies*. The microsite types 'Logs', 'Branches' and 'Coarse Woody Debris' (CWD) will cover a maximum of 30% of the area on both the montane and the subalpine level (Figure 7a and b).

On the subalpine level, mosses will probably be dominant only for a few additional years. Afterwards, microsite types with ferns will quickly become dominant, while grasses will always co-dominate (Figure 7b). These simulation results suggest that *Picea abies* will establish at the subalpine level much more slowly than at the montane level (Figure 7).

Discussion

Model accuracy for two successional pathways

The two elevational levels on the Gandberg site in the northern Swiss Pre-Alps represent case studies for two of the most frequent successional pathways after beetle-caused conifer tree die-back, with an invasion by *Rubus idaeus* at the montane level as opposed to a strong dominance by *Calamagrostis villosa* and ferns at the subalpine level. Our model was developed (i) to reproduce the observed snag decay and vegetation patterns on both elevational levels and (ii) to project future short-term succession patterns. The first goal was achieved accurately at both the montane and the subalpine level (Figure 6). Thus, we conclude that the modified matrix-model approach used here is quite powerful for such purposes.

The most common criticism of matrix models is their assumption of stationarity of the transition parameters (cf. Usher 1981). For the specific case of matrix models investigated here, however, the assumption of stationarity is probably not critical, because the model is used only for a relatively short period (i.e. max 25 years of simulation). Vegetation dynamics in mountain forest tend to be much slower than at low elevations, and hence changes such as tree canopy development that would violate the assumption of stationarity of the parameters are unlikely to occur during the simulated time. In addition, the most strongly varying transition processes (e.g., from all the non-woody microsite types into 'Logs' and 'Branches') were treated with an approach that differs from that of a standard matrix model (i.e. distinction between woody and non-woody microsite types). Nevertheless, due to the nature of our database, it was

difficult to estimate the transition probabilities into some microsite types that will become quantitatively more important in the future, such as pioneer trees and 'Picea' (cf. sensitivity analysis).

For the montane level, the model suggests that *Rubus idaeus* will be replaced by *Picea abies*. This projection is corroborated by the fact that pioneer trees were absent almost entirely in the early succession on the Gandberg site, whereas *Picea* saplings were already present under *Rubus* in 2001 (Kupferschmid et al. 2002). However, such a succession is likely to happen only where advanced tree regeneration is present, or where *Picea* mast years occur in surrounding stands in the first few years after the beetle attack. If tree regeneration does not establish quickly after tree die-back, competition by ground vegetation may be too strong for *Picea*, and the *Rubus idaei* associations will probably dominate much longer. Thus, a fast succession towards a new tree stand requires 'windows of opportunity', which conforms with findings from several other studies (cf. Bugmann and Weisberg 2003; Sage et al. 2003). As a corollary, we conclude that it is quite important to model tree regeneration in more detail, and we will focus on this problem in a companion paper (Kupferschmid et al. submitted for publication).

For the subalpine level, it was considerably more difficult to make appropriate assumptions for the long-term simulation. If our assumptions are correct, ferns and grasses will be the dominant species for a fairly long period into the future (Figure 7b). In addition, more than 20% of the surface will be covered by logs and coarse woody debris 20 years after tree mortality (Figure 7b). It can be expected that the rotten wood and stumps will be important as 'safe sites' for tree regeneration in the coming decades (cf. Reif and Przybilla 1995, Szewczyk and Szwargrzyk 1996; Nüsslein and Faisst 1998; Ulanova 2000). However, the amount of future *Picea abies* recruitment on coarse woody debris will depend mostly on the availability of seeds and therefore on the seed production of the few surviving mature trees, or on long-distance seed transport from the adjacent living stands. Again, this underlines the importance of modelling tree regeneration in more detail.

Although it is clear that long-term simulation studies with the model would gain plausibility if seed dispersal, tree germination, growth and mortality were modelled explicitly, we conclude that the model presented here demonstrates that it is possible to accurately simulate wood-decay and ground vegetation patterns based on rather simple assumptions, and to provide a good basis for projecting the temporal development of these montane and subalpine snag stands.

When to use which model parameter set?

It would be desirable to be able to predict from certain criteria which succession will take place directly after the die-back of trees, (1) *Rubus idaeus* invasion or (2) mosses followed by *Calamagrostis* and fern dominance. Based on such knowledge, the 'montane' matrix (Table 2) could be used to simulate a *Rubus* invasion, and the 'subalpine' matrix (Table 3) for the succession with dominance by ferns and grasses. However, at the moment such criteria are missing, and a user of our model has to choose between the two separate transition matrices.

We can only speculate about the reasons for the invasion of *Rubus idaeus* that occurred at the montane level, but not (yet) at the subalpine level of the Gandberg site. Often, *Rubus idaeus* has been observed to quickly invade a site by sexual reproduction after disturbance, whereas *Rubus* invasion by vegetative spread would be a much slower process. Peterson and Carson (1996) proposed that the abundance of characteristic seed-bank pioneer species such as *Rubus* spp. is dependent on propagule availability, which in turn is determined by forest age and size (Peterson and Carson 1996). In experiments, fresh seeds of *Rubus idaeus* did not germinate easily (Giannini 1972), but if the seed coats had been damaged during long-term storage in the seed bank and/or had experienced years of scarification, *Rubus* seeds germinated well (Lautenschlager 1997). We thus conclude that 'old' seeds from a former *Rubus* scrub are conducive to a fast *Rubus* invasion after tree die-back. This was probably the case at the montane level of the Gandberg site, as this site had been clear-cut in the 19th century. Furthermore, according to Lautenschlager (1997), *Rubus* seedlings will establish and expand successfully only where ample light, nutrients and moisture are available. Such conditions are commonly met following harvesting, windthrow (Fischer and Jehl

1999) and probably also after beetle infestations. It is not clear whether the lack of *Rubus* dominance in some sites (e.g., Yeager and Riordan 1953; Baker and Kemperman 1974; Schulz 1996; Wurz and Wahrenbrock 2000) may be due to the absence of historical clear-cutting or ecologically similar disturbances. However, in sites above a certain elevation and probably also in pristine forests where grasses were present before tree dieback, *Rubus* seemed to be restricted mostly to the scattered mounds of uprooted trees (Jehl 1995; Reif and Przybilla 1995; Heurich 2001; Kupferschmid 2001).

According to Lieffers and Stadt (1994), *Calamagrostis canadensis* was virtually eliminated from stands or was greatly reduced when only 10 or 40% of full sunlight was available at the forest floor. As *Calamagrostis canadensis* and *C. villosa* are ecologically comparable, we surmise that on the Gandberg site, *Calamagrostis* was probably absent in the dense stands at the montane level prior to the beetle attacks (growing stock of about 820 m^3/ha, Kupferschmid Albisetti et al. 2003). However, in the more open stands at the subalpine level (590 m^3/ha, Kupferschmid Albisetti et al. 2003), it is likely that *Calamagrostis* had already dominated the open places before the death of the trees (Figure 2, grey bars). Eight years after tree mortality, grasses were still restricted to these areas and actually could not expand (Figure 2, white bars). This is in contrast to beetle-killed stands in Colorado, where grasses and sedges had nearly twice the density in stands with dead trees compared to stands with living trees (Yeager and Riordan 1953).

Generally, the model structure we used is suitable to reproduce such successional patterns. Particularly, we conclude that our model with the transition matrix parameterised for the montane level can be used to simulate the succession in beetle-killed stands that are vulnerable to *Rubus* invasions, such as (1) dense stands that have been exposed to clear-cuts or heavy disturbances in the past, (2) stands that already have some *Rubus* patches, or (3) stands that lack a dense ground vegetation cover, in particular where grasses and sedges are rare or even absent. In contrast to the 'montane' parameterisation, our model with the transition matrix parameterised for the subalpine level can potentially be used to simulate ground vegetation succession in other beetle-killed

Norway spruce stands. Yet, this empirical model approach would have to be adapted to new locations by at least partly re-parameterising the transition matrix and the decay parameters. Additional work would be required to derive a more generally applicable model. Nevertheless, we conclude that the present modelling approach can be quite helpful to summarise and synthesize field data and to project the decay and ground vegetation development in a quantitative manner into the future.

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