

Using a retrospective dynamic competition index to reconstruct forest succession

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Abstract

Understanding forest dynamics and stand structures is crucial for predicting forest succession. However, many forests have been altered due to century-long land-use practices, which complicates the reconstruction of past and current successional trajectories. For a better understanding of successional processes, we suggest studying the intra- and interspecific competition among single trees across time. We introduce a tree-ring based competition index to reconstruct the competitive dynamics of individual trees over time. This new retrospective dynamic competition index combines a temporal and a spatial component by calculating the yearly ratio between the basal area increments (bai) of the neighbouring trees and the subject tree. The new index is applied to mixed Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) stands in the inner-Alpine dry-valley Valais, for which a change in species composition is hypothesised. The aim is to analyse current stand structures in terms of recent changes in the competitive interactions at the single tree level and to relate these competitive dynamics to land-use change and increasing drought due to climate change. On five plots, the positions of 456 trees were recorded and increment cores were taken to derive bai data. The individual dynamic competition index curves were aggregated in clusters, which define typical patterns of competitive dynamics in both tree species. A large percentage of the trees (87% in oak, 70% in pine) were clustered into a group of trees with constant competition at a relatively low level. However, a smaller group of pines (20%) had recently faced increasing competition. In addition, stand structure analyses indicated a change towards a higher proportion of oak. This change in the competitive ability between oak and pine was found to be related to drought, in that oak had a competitive advantage in dry years. Furthermore, the high proportion of dead branches in pines with decreasing competitive abilities indicated increasing competition for light as a consequence of natural development towards a later successional stage that favours the more shade-tolerant oak. The new retrospective dynamic competition index proved to be promising in studying forest succession. The tree-ring based method allows us to identify changes in the competitive ability of single trees with a high temporal resolution and without repeated assessments.

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1. Introduction

Intra- and interspecific tree competition is an important factor in forest succession. By definition, competition is “an interaction between individuals, leading to a reduction in the survivorship, growth and reproduction of the competing individuals concerned” (Begon et al., 1996). In forest succession, competition is assumed to play a major role in species replacement (Bazzaz, 1996). Disturbance is viewed as a mechanism for initiating succession (Bazzaz, 1996) and can have a long-term effect on stand development and successional pathways (Oliver and Larson, 1996) by changing competitive

dynamics among trees. When predicting future forest development, reconstructing past disturbance regimes and identifying changes in competitive interactions are key issues. Understanding the dynamics of forest stands with strong past anthropogenic disturbances is particularly difficult because the different types of human impact typically vary in time and space.

Many forests have been altered over centuries by historical land-use practices. However, for economic reasons, a large part of the forests in Europe has been abandoned since the second part of the 20th Century, and natural succession is now proceeding. Furthermore, global change is altering site conditions, and with it forest productivity and species composition (cf. Bugmann, 1997; Jarvis, 1998; Shugart, 1998; IPCC, 2001). As a consequence, the future growth and stand

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dynamics of these forests are likely to differ from past trajectories (Spiecker, 1999). Investigating the changes in structure and species composition of these forests is a scientific challenge because the initial state is often unknown and the successional pathways are complex. The present paper addresses these issues, using the competitive dynamics of Scots pine (*Pinus sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) in the formerly heavily exploited forests of Valais, an inner-Alpine dry valley in Switzerland, as a case study. These forests are currently characterized by high pine mortality and the expansion of oak, which seems to be related to land-use change and increasing drought due to climate change (Rebetez and Dobbertin, 2004; Weber et al., in press).

Forest development is most promisingly studied by following the fate of individual trees (Harper, 1977). Tree-rings provide a tool to retrospectively trace the growth of individual trees. They contain information not only on the climatic growing conditions, but also on the competitive level of a tree (Cook, 1990). Competitive interactions between individual trees are usually reflected in periods of growth suppression and release (Banks, 1991). In the last two decades, dendroecologists have often used release identification methods to reconstruct disturbance events and stand dynamics in forests (e.g. Lorimer, 1980; Payette et al., 1990; Frelich and Reich, 1995; Abrams et al., 1998; Bergeron, 2000; Motta et al., 2002; Black and Abrams, 2003; Beber et al., 2004; Gutierrez et al., 2004; Rubino and McCarthy, 2004). These analyses have proven useful in detecting the magnitude and frequency of disturbances (Black and Abrams, 2003) and the general patterns of the species-specific responses during succession at the stand level. They seem, however, to be less appropriate for evaluating the intra- and interspecific competitive ability of individual trees, which can vary considerably over time. Moreover, focusing on successional trajectories over time, these analyses have hardly ever considered spatial relationships among single trees. Such spatial relationships have, however, been found to strongly affect the stem growth of individual trees (Biondi et al., 1994; Parish et al., 1999), and could therefore help to explain the growth patterns of uneven-aged and uneven-structured stands, such as those of abandoned forests.

In contrast, spatial interactions among individual trees have normally been investigated using static competition indices, which are lacking a temporal component. There is a long tradition of such distance-dependent analyses of competition, in which the current growth of a target tree is analysed as a function of the size ratios with and the distances from the neighbouring competitor trees (e.g. Hegyi, 1974; Daniels, 1976; Tome and Burkhart, 1989; Biging and Dobbertin, 1992; Stoll et al., 1994; Vacek and Leps, 1996). These studies have shown a close relationship between competition indices and tree growth. However, these classic competition indices have the disadvantage that the dynamics of the system cannot be represented (Burton, 1993).

Our overall goal is to present a novel index to retrospectively trace competition of individual trees. This “retrospective dynamic competition index” combines a temporal and a spatial component by comparing growth rates of a subject tree with

growth rates of neighbouring trees. The specific objectives of our study are (1) to define different patterns of retrospective dynamic competition in oak and pine trees; (2) to compare these patterns with classically used static competition indices and growth parameters; (3) to examine them together with stand structure in terms of successional changes in the low-elevation forests in Valais; (4) to analyse how drought influences differently the competitive ability of pine and oak across time.

2. Materials and methods

2.1. Study area

The study was carried out in Valais, an inner-Alpine dry valley situated in the south-western part of Switzerland (Fig. 1). The east–west oriented valley is characterised by a subcontinental-dry climate with high insolation. Precipitation is fairly low (between Visp and Sion less than 600 mm per year) because of the rain shadow exerted by the high mountain ranges in the South, Southwest and the North of the valley. Valais is known as the driest region in Switzerland and as one of the driest inner-Alpine valleys (Braun-Blanquet, 1961; Ozenda, 1985).

In Valais, human impacts on past stand dynamics have been manifold. In the 19th Century, large parts of the forests were devastated by foreign armies and by local communities to extract export timber, firewood and railway timber (Meyer, 1950, 1951, 1952; Kempf and Scherrer, 1982). For hundreds of years, goat grazing (Stuber and Bürgi, 2001) and litter clearance (Stuber and Bürgi, 2002) were widespread land-use practices that resulted in fairly open forest stands and in the suppression of the preferentially browsed (Mayer, unpublished data) oak trees. The regeneration of oak was additionally hampered because the acorns were removed by litter collecting. In contrast, the clear-cuttings of the 19th Century and the use of wooded pastures facilitated the establishment of the light-demanding pioneer pine species.

However, after a few decades of abandonment, a change in the species composition of these forests is becoming apparent.

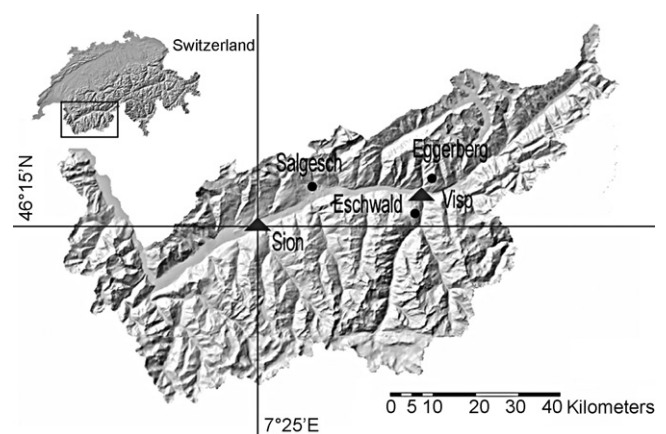


Fig. 1. Geographic position of the study area in Valais. The climate stations of Visp and Sion are indicated by grey triangles, and the study sites at Eschwald, Eggerberg and Salgesch by black dots.

While oak is spreading (1983–1993: +30% in stem number, WSL, 2001), the annual mortality rates of pine at low-elevation sites are up to twice as high as the 0.4–0.5%, which are usually observed in managed forests in Switzerland (Dobbertin et al., 2005b). At present, pine and oak form extensive mixed stands in Valais's low-elevation forests (below 1200 m a.s.l.). Besides land-use change, changes in climate, i.e. a higher number of hot days (Rebetez and Dobbertin, 2004) and different seasonality in moisture availability (Weber et al., in press) are thought to play a role in the competitive dynamics between pine and oak. Oak may benefit from its ability to adapt to drier conditions, whereas pine appears to suffer from prolonged summer drought conditions and the increasing abundance of phytopathogens, insects and mistletoes (Rigling et al., 2004; Dobbertin et al., 2005a; Weber et al., in press).

2.2. Study plots

In the lower montane pine forest belt of Valais, five forest plots were studied, each of which with an area of 452 m². They were selected so as to represent typical forest stands at low elevations. The study sites were situated between 710 and 1075 m a.s.l., where the vegetation is a mixture of dominating pine (*Ononido-Pinetum*, *Odontito-Pinetum* and *Ericeto-Pinetum*; Braun-Blanquet, 1961; Plumettaz Clot, 1988) and an increasing fraction of oak forest associations (*Saponaria-Quercetum pubescentis*; Burnand, 1976). The plots were chosen in those areas that showed a comparatively high oak proportion and potentially seemed to be most affected by changes in climate and land use (i.e. xeric site conditions, evidence of past forest management). Only by evaluating such later successional stages of mixed pine and oak stands, was it possible to estimate the competitive ability of pubescent oak in formerly pine-dominated forests. In compliance with these conditions, we chose two mixed pine and oak plots at Eschwald (46°15'35"N, 7°52'40"E), one plot at Eggerberg (46°18'50"N, 7°54'20"E) and two plots at Salgesch (46°19'25"N, 7°33'40"E) (Fig. 1).

The Eschwald and Eggerberg plots are located in the Visp sub-region where the annual rainfall amounts to 599 mm at the Swiss Meteorological Institute (SMI) climate station of Visp for the period 1961–1990. The Salgesch plots belong to the Sion sub-region, with an annual rainfall of 598 mm at the nearby SMI climate station of Sion. However, between Visp and Sion, the precipitation sum from June to August increases from 123 mm to 162 mm, indicating less continental conditions in the Sion sub-region.

2.3. Field sampling and processing of tree-ring data

On each of the five sampling plots, which were 12 m radius (=452 m²), all the oak and pine trees with a minimum diameter at breast height (dbh) of 5 cm and a minimum height of 3 m were georeferenced and cored using an increment borer. Two cores were taken at breast height to analyse growth and to derive competitive dynamics, and one core was extracted at the base of each tree to determine its age. Damaged trees, tree

stumps and dead trees were cored if possible and marked as such.

For each tree, height (*h*), dbh, social class (soc: 1 = dominant, 2 = codominant, 3 = subdominant, 4 = suppressed (cf. Kraft, 1884)), and height proportion of crown to stem (cpr: 1 = low proportion, 4 = high proportion) were recorded. Additionally, for pine trees, the height proportions of stem with dead branches to total stem height (dbr: from 1 = low proportion to 9 = high proportion) were estimated as a measure for light competition (Makinen and Colin, 1999).

Tree rings were measured on a Lintab3 measuring system (F. Rinn S.A., Heidelberg, Germany) with a resolution of 0.01 mm. The TSAP tree-ring software (Rinn, 1996) was used to crossdate the cores (Fritts, 1976; Schweingruber, 1988). Tree-ring data from all the trees sampled could be successfully used for the further analyses, although measuring and cross-dating the sometimes strongly suppressed trees at these rather extreme sites was fairly difficult. The ring widths of the two cores of each tree were averaged and converted to basal area increment (bai) since bai is mathematically less biased by stem geometry, which makes it less dependent on tree age. Bai is also a better estimate for the effective resource exploitation of a tree.

2.4. Analysis of competitive dynamics

Using bai data, we derived a retrospective dynamic competition index to analyse the competitive ability of individual oak and pine trees over time. The index calculation was based on the assumption that high bai growth values imply a high competitive ability (Bazzaz, 1996; Begon et al., 1996). Correspondingly, trees with high bai exert competitive stress on neighbouring trees with lower bai values. Trees from the same stand usually show a common signal in their tree-ring series (Fritts, 1976), which is related to climate and therefore has been the focus of many dendroclimatological analyses. In our investigations, however, we were not interested in extracting this common signal, but in explaining the differences in the individual growth patterns. Thus, we calculated bai ratios of neighbouring trees over time, which resulted in the partial removal of the common climate signal.

To avoid edge effects, the analysis was performed for all the trees in an inner circle 9.5 m in radius on each plot, since we used a circular neighbourhood zone 2.5 m in radius around each single investigated tree. This relatively small size of the neighbourhood zone was justified by the comparably low maximum tree height and the fairly open forest stands. Within this neighbourhood zone, competition was expected to be distance-dependent, i.e. to decrease linearly with increasing distance from the investigated subject tree. Based on the above requirements, we calculated the retrospective dynamic competition index as follows:

$$C_{i,t} = \sum_{j=1}^n \frac{\text{bai}_{j,t} / \text{bai}_{i,t}}{\text{dist}_{ij}}$$

where $C_{i,t}$ is the competition load for the subject tree i in the year t , $\text{bai}_{j,t}$ the basal area increment of the competitor tree j in

the year t , $\text{bai}_{i,t}$ the basal area increment of the subject tree i in the year t , dist_{ij} the distance between the subject tree i and the competitor tree j , and n is the number of competitors in the neighbourhood zone. If a subject tree has zero competitors, the index takes a value of 0. In all other cases, the index becomes higher the more competitors a subject tree has, and the better these competitors grow in comparison to the subject tree. When tracing the development of the competition index over time, we speak of the “competitive dynamics” of a tree, which is characterized by the level of competition the tree faces, i.e. the value of $C_{i,t}$, and the trend in competition over time. Both level and trend in competitive dynamics across time were explored by plotting annual cumulative curves of the competition index over time.

The level of dynamic competition did not differ significantly between the two species when comparing intraspecific (oak with oak, pine with pine neighbours) with interspecific competition indices (oak with pine, pine with oak neighbours). The influence of a competitor oak or pine tree was therefore assumed to be equal. The analysis was done for the time span 1960–2001, since most trees were older than 40 years and the period was long enough to detect changes in competitive relationships but short enough to find evidence of management activities (stumps) and mortality (dead trees) on each plot.

2.5. Clustering trees with similar competitive dynamics

All the competition curves of the single trees from the five plots were analysed in combination. To reveal different patterns of competitive dynamics within the sampled trees, we performed a cluster analysis. Thereby the aim was to define groups of individual trees with similar patterns regarding their level and trend of competition load across time. In a first step, we therefore calculated annual cumulative curves from the dynamic competition index for each single tree by adding up the competition load of a particular year to the sum of the previous years. With these individual trees’ annual cumulative curves of the competition index as input data, we applied the average linkage method with Euclidian distance using the statistics software R, version 1.6.2 (R Development Core Team, 2003) for clustering, for oaks and pines separately. Based on the resulting dendrograms, groups of trees with similar competitive dynamics were distinguished. For each of the resulting groups, we calculated an average annual cumulative competition curve.

For comparison with the retrospective dynamic index, two static competition indices and three additional growth parameters were calculated for the sampling year 2002. The classic distance-dependent competition index that was introduced by Hegyi (1974) was calculated as follows:

$$CI_{1i} = \sum_{j=1}^n \frac{\text{dbh}_j / \text{dbh}_i}{\text{dist}_{ij}}$$

where CI_{1i} is the competition index for the subject tree i , dbh the diameter at breast height, dist_{ij} the distance between the subject tree i and the competitor tree j , and n is the number of competitors in the neighbourhood zone.

Furthermore, we introduced a competition index that focuses on tree height compared to the competitors’ height. This index was calculated as follows:

$$CI_{2i} = \frac{\sum_{j=1}^n H_j}{n}; \quad \text{if } (h_i > h_j) \Rightarrow H_j = 1; \text{ else } \Rightarrow H_j = 0$$

where CI_{2i} is the competition index for the subject tree i , h_i the height of the subject tree i , h_j the height of the competitor tree j , and n is the number of competitors in the neighbourhood zone. The resulting index is 1 if the tree is taller than all its competitors; it is 0 if the tree is smaller than all its competitors and ranges between 0 and 1 in the other cases.

The additional three parameters are based on growth rates and were chosen as supplementary measures for the competitive ability of a subject tree. Sapwood area (sap) is known to be related to leaf area (Grier and Waring, 1974) and was calculated by summing up the basal area increment of the sapwood rings. Bai_{10} was calculated as the sum of the basal area increment over the last 10 years. Finally, relbai , the ratio between bai_{10} and total basal area of the subject tree, was added as a relative measure of its growth capacity. The resulting values were also averaged according to the clusters of the dynamic indices for comparison.

2.6. Competitive dynamics and drought

The patterns of the competitive dynamics of the pines were compared to those of the oaks by calculating the interval trends (Schweingruber, 1988, 1990) with the individual trees’ retrospective dynamic competition curves. For the interval trend, the number of ascending and the number of falling curves for each year-to-year interval was recorded. The percentage of ascending intervals within the dynamic competition curves of the pines was subtracted from the percentage of ascending intervals within the curves of the oaks. In the resulting curve, values above 0 mean a competitive advantage for the pines, whereas values below 0 mean a competitive advantage for the oaks. This difference curve of competition was evaluated against the drought index DRI (Bigler et al., 2006) across time to reveal whether drought as a limiting factor influences the competitive dynamics of oak and pine. DRI was calculated as the difference between precipitation and potential evapotranspiration according to Thornthwaite (1948). For the two sub-regions Visp (Eschwald and Eggerberg) and Sion (Salgesch), separate drought indices and separate interval trends of competitive dynamics were computed. The interval trends were analysed between 1970 and 2001 because the number of trees used for the analysis (replication) was fairly constant during that period.

3. Results

The age and dbh structure of all the trees on the 5 sampling plots indicated a change in species composition towards oak (Fig. 2), as pine was more frequent in the upper dbh and age classes, whereas oak was noticeably more abundant in the lower

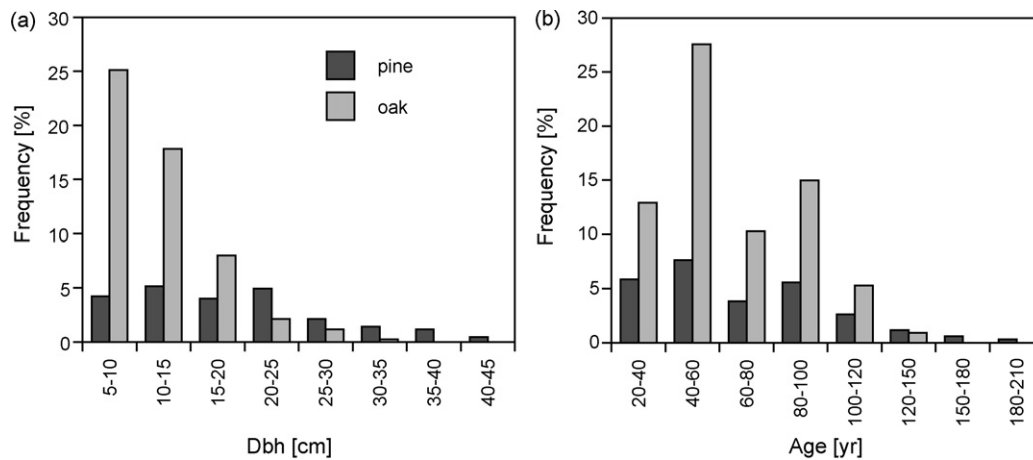


Fig. 2. Dbh (a) and age histograms (b) for all the trees on the five sampling plots. Only pine (no = 126) and oak (no = 300) trees with a dbh greater than 5 cm and a height above 3 m were considered.

dbh and age classes. (Note that the lowest age class (20–40 years) does not constitute a representative sample because trees with a dbh smaller than 5 cm and a height smaller than 3 m were not included.)

A total of 456 trees were cored, measured and cross-dated. The sample sizes, the numbers of dead trees and stumps, and the total number of trees taller than 3 m are listed for each plot separately in Table 1. Overall, 19 pine stumps and two dead pine trees were recorded that could not be cored due to advanced wood decay (Table 1). As wood decay is quite slow in such dry climates, we can assume that these trees died before the period of analysis. Additionally, three oak stumps could not be sampled, two of which were not a neighbour of any tree analysed in the competition analyses.

In the inner circles 9.5 m in radius, 132 oak and 40 pine subject trees could be analysed for retrospective dynamic competition, reflecting the abundances of the two species in the forests studied. The individual trees' cumulative dynamic competition curves were grouped according to similar patterns,

for pine and oak separately. The clustering procedure divided the curves into well-defined clusters (Fig. 3).

For both species, a large percentage of the trees (87% of the oak, 70% of the pine trees) revealed very similar competitive dynamics, i.e. constant competition on a relatively low level (Fig. 4). These trees were considered as one group (oak1, pine1) and were not subdivided any further to emphasise their difference from the other competitive patterns. One single oak tree was excluded from the further analysis steps because it made up a cluster of its own. In this way, four patterns of competitive dynamics were identified for both pine and oak, ranging from a low (oak1, pine1) to a high competitive level (oak4, pine4) (Fig. 4). For oak, the competitive patterns generally were consistent with the current values of the static competition indices and the other growth parameters (Fig. 4, refer to CI1, CI2 and parameter list). As an exception, oak3 (3 trees) would be classified as being suppressed more strongly than oak4 (2 trees) based on dbh, height, social class and also the height-dependent index CI_2 . Except for the first 10 years of

Table 1
Number of trees sampled (top) and selected stand structure parameters (bottom) for the five plots in Valais. For the stand structure parameters, stem numbers and basal areas were extrapolated from the plot area (452.4 m²) to 1 ha

Number of samples	Eschwald lower	Eschwald upper	Eggerberg	Salgesch lower	Salgesch upper	Total
Living oaks	30	36	50	110	74	300
Living pines	14	56	12	22	22	126
Stumps: total/not sampled	13/3	16/11	2/2	4/4	2/2	37/22
Dead pines: total/not sampled	2/0	10/2	1/0	1/0	3/0	17/2
Stand structure parameters	Eschwald lower	Eschwald upper	Eggerberg	Salgesch lower	Salgesch upper	Mean
Number of oaks (ha)	663	796	1105	2432	1636	1326
Number of pines (ha)	309	1238	265	486	486	557
Basal area/ha (m ²) for oak	12.01	6.32	8.31	5.42	5.95	7.6
Basal area/ha (m ²) for pine	9.64	7.76	4.26	4.42	5.31	6.3
Maximum height oak	16.7	14.5	11.8	10.4	11.9	13.1
Maximum height pine	18.7	11.2	12.6	9.9	9.4	12.4
Maximum dbh oak	33.5	26.5	19.5	17.5	19.0	23.2
Maximum dbh pine	38.0	22.0	36.0	27.0	28.0	30.2
Maximum age oak	120	96	46	90	121	94.6
Maximum age pine	89	111	86	150	203	127.8

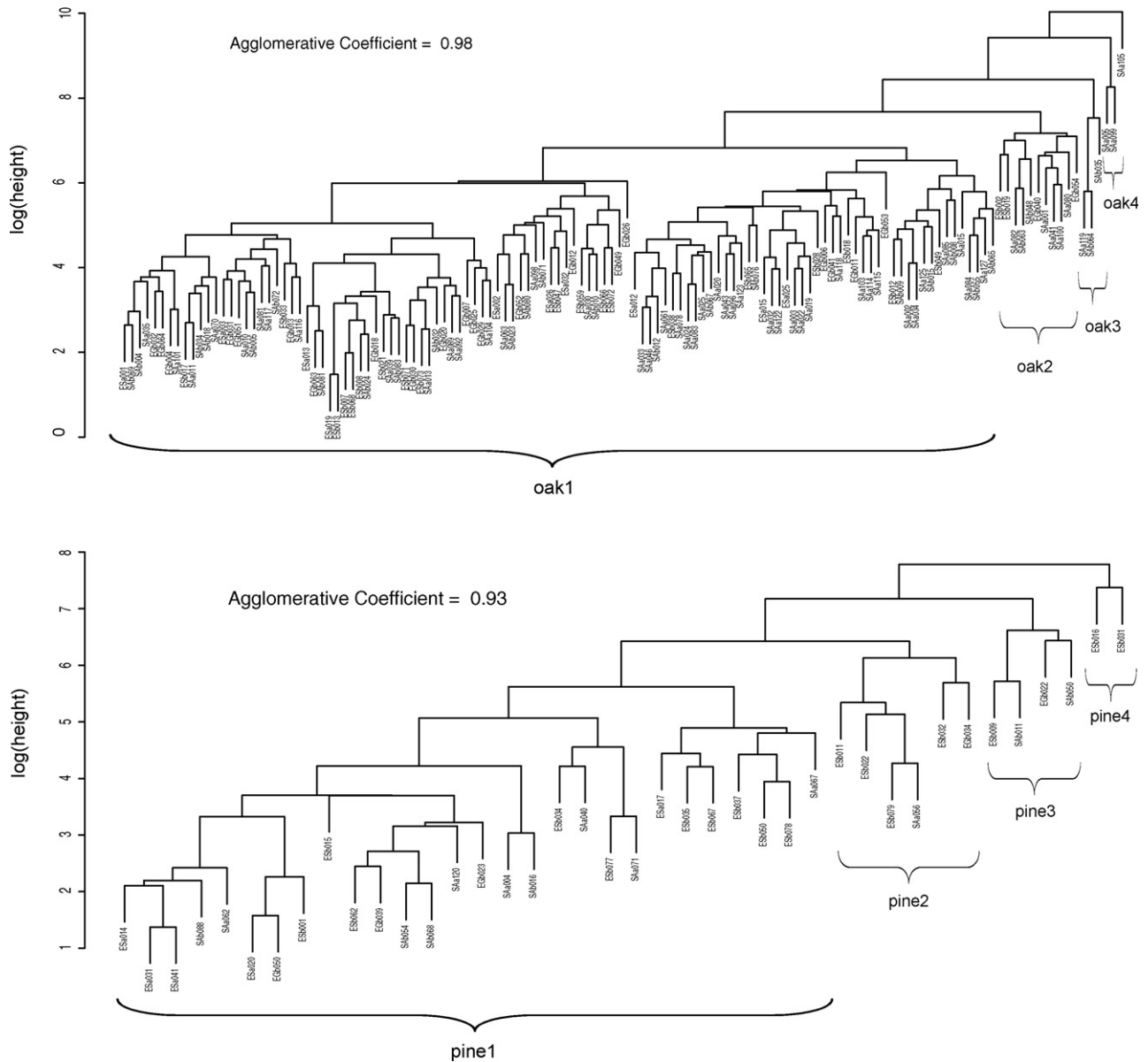


Fig. 3. Clustering of the cumulative retrospective dynamic competition indices of pines and oaks by average linkage. The height axis was log-transformed. Four clusters were segregated for both species (oak1–4, pine 1–4).

oak4, the oaks showed nearly straight competition curves, i.e. no notable increase in competition during the investigated period. The dynamic competition index for oak3 and oak4 even flattened during the last 10 years, indicating a slight decrease in competition. Among the four competition levels in pine, pine2 (6 trees) and pine4 (2 trees) showed a pronounced increase of competition during the last 10 years. In fact, most current growth parameters (soc, cpr, dbr, sap, bai10, relbai) suggested that today, pine2 had a lower competitive ability than pine3. In particular, the proportion of dead branches as a measure for recent crown competition was higher in pine2, being nearly as high as in pine4. Unlike the dynamic indices, the static competition indices CI_1 and CI_2 concealed the increasing competitive pressure on the trees in pine2.

In comparison to basal area increment (bai), the competition index contained rather different information. If we had looked

at bai alone (Fig. 5), the trees would not have been grouped into the same clusters as for competition, since the bais of trees within the clusters varied markedly. For example, both in the high-competition clusters oak4/pine4 and in the low-competition clusters oak1/pine1, some trees had very slow growth. Nevertheless, some general patterns in bai were visible. Trees in cluster pine1 grew well in the period 1965–1985, but growth decreased in many trees during the last 15 years. A similar pattern was found in pine2 and pine4. Only the trees of cluster pine3 grew better after 1975. In contrast, the average growth of all four oak clusters increased over time, most markedly after 1975. The oaks nevertheless displayed smaller average bais than the pines.

Oaks tended to have a larger height at a certain dbh (Fig. 6) and to grow better at a given dbh (Fig. 6), although the differences were statistically not significant (test for homogeneity

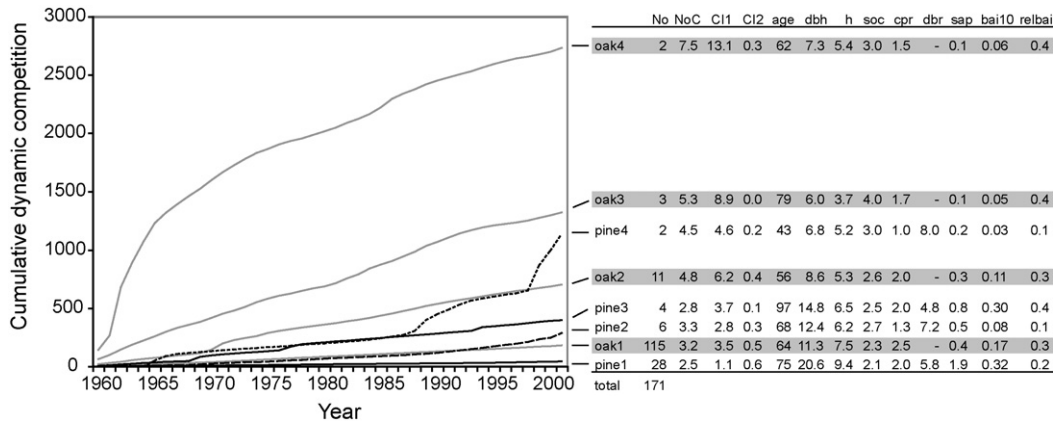


Fig. 4. The four competitive patterns of oak (grey) and pine (black) trees. Cluster averages of the cumulative retrospective dynamic competition indices (diagram left) are compared to the cluster averages of the static competition indices (CI₁ and CI₂) and the other growth parameters in the year 2002 (table right). Parameter descriptions: No is the number of trees in each cluster; NoC the average number of competitors for subject trees belonging to a certain cluster; CI₁ and CI₂ the competition indices; *h* the tree height (m), soc the social class (1, dominant; 2, codominant; 3, subdominant; 4, suppressed); cpr the crown proportion (lowest class: 1, highest class: 4); dbr the dead branches along the stem (1, low proportion; 9, high proportion); sap the sapwood area (cm²); bai10 the basal area increment of the last 10 years (cm²); relbai is the ratio between bai10 and total basal area.

of slope; Sokal and Rohlf, 1995). In 2002, most of the oaks had a dbh smaller than 25 cm. In the future, these differences in the dbh-height relation between pine and oak may therefore gain significance. Contrary to our expectations, neither tree height nor basal area increment of the last 10 years (bai10) were related to tree age (Fig. 6).

Oaks and pines differed in their interval trends of ascending competition over time (Fig. 7). The difference curve of the

interval trends partially ran parallel to the drought index DRI. The correlation between the two curves was fairly good for trees in the Visp sub-region ($r = 0.43$), but it was lower for trees in the Sion sub-region ($r = 0.31$). A competitive disadvantage of the pines often coincided with dry years (i.e. low DRI), whereas a competitive disadvantage of the oaks was less frequent, and was often observed in or just after moist periods (i.e. high DRI). Overall, the curves tended to be more similar in

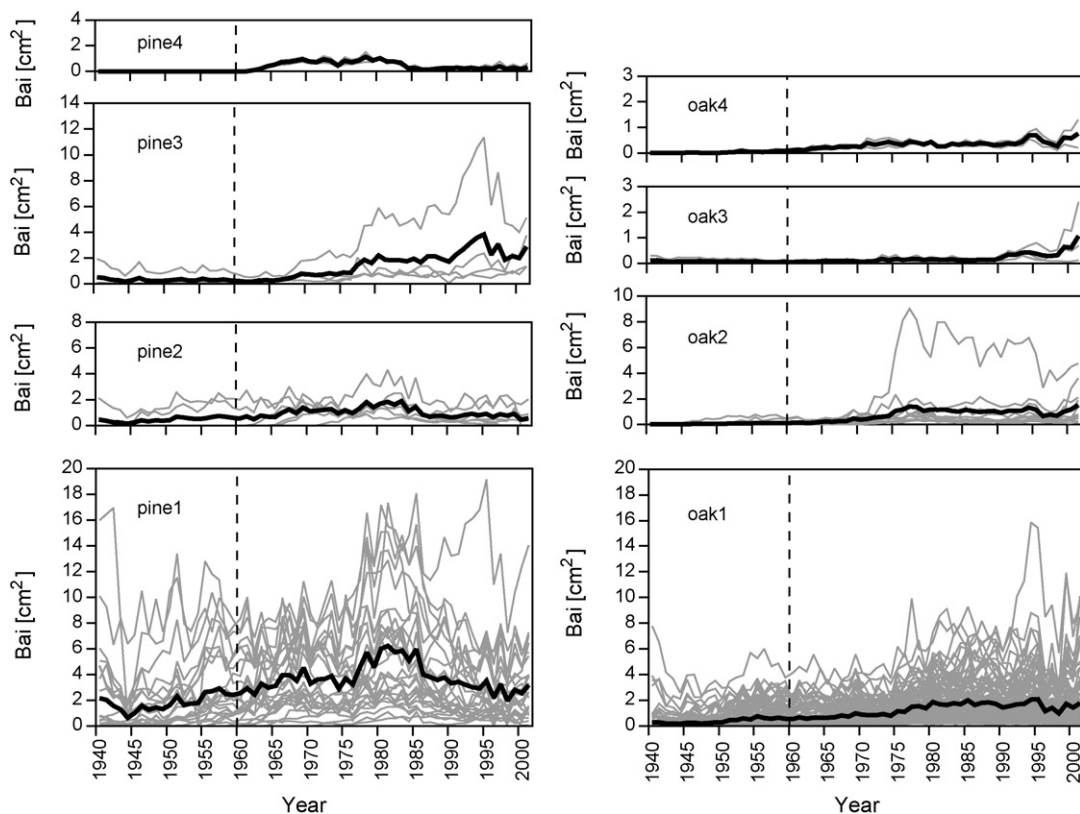


Fig. 5. Basal area increment (bai) of all subject trees grouped according to the four competition clusters in oak and pine. Thick black line: average bai of each cluster. The dashed line marks the start of the period of dynamic competition analysis.

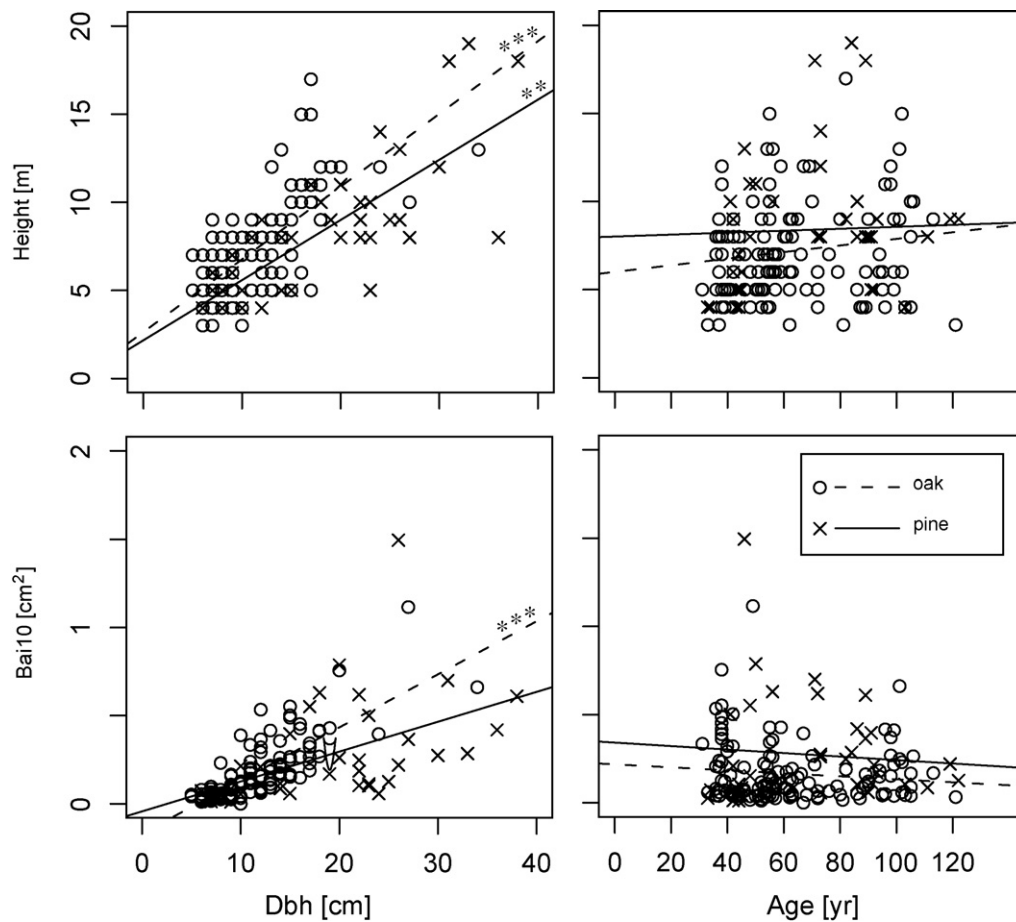


Fig. 6. Differences in the growth of oak and pine. Height and bai10 (basal area increment of the last 10 years) show a relationship with dbh (left), but not with age (right). Significance of the linear model: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

the second half of the investigated period. The interval trend did not show a clear trend in the competitive regime between pine and oak over the 30-year period.

4. Discussion

4.1. Reconstruction of competitive dynamics

By using a retrospective dynamic competition index and clustering the trees according to the similarity of competitive patterns (Figs. 3 and 4), we were able to distinguish three major competitive patterns, which provide useful information on stand dynamics in addition to those obtained using static indices. First, a majority of the trees shows relatively constant competition over time (linear cumulative competition curves). Second, some trees can be found with recently increasing competition (cumulative curves deviate from linear course: pine2 and pine4). Third, some trees are growing under a high competition regime even though constant over time (curves with a comparably large slope: oak3 and oak4).

Unlike many studies on the stand structure of mixed forests, we found that height and basal area growth are not related to tree age for both pine and oak (Fig. 6). This result is indicative of the highly variable tree growth in these stands, which on the one hand has been altered strongly by past land-use practices

(Rigling et al., 2004), and on the other hand is constrained by the xeric site conditions (Rigling et al., 2002; Weber et al., in press). In these forests, we find various tree growth forms: both young and old trees can be suppressed (i.e. small size and low growth rates) or become dominant (i.e. large size and high growth rates) (Fig. 6). Given this variability of growth forms, the new method was needed for analysing the competitive abilities of single trees over time.

With respect to both the static and the dynamic competition indices, oaks seem to be more constant in their competitive ability in the long-term, whereas some pines show inconsistent competitive patterns (Fig. 4). As a consequence, further growth declines of some pine trees can be expected, thus emphasising the change in species composition that is evident from the basic stand structure analyses (Figs. 2 and 6).

4.2. Competition as a factor for forest succession in Valais

A change in species composition towards a higher oak proportion is evident from the analyses of stand structure and both the dynamic and static competition indices. The reasons for the observed change are manifold and complex (Rigling et al., 2004; Weber, 2005). However, the major drivers underlying the currently observed successional processes are changes in land use. Historical land-use activities, which

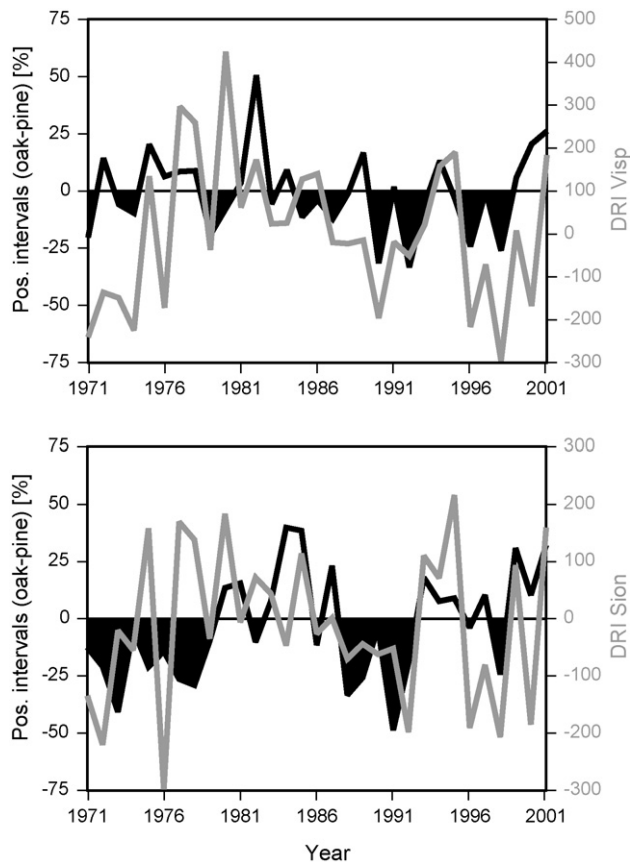


Fig. 7. Difference curve of positive intervals in the competitive dynamics of oaks and pines (black) compared with the yearly drought index DRI (grey). Eschwald upper and lower plot and Eggerberg belong to the Visp sub-region (top), Salgesch upper and lower plot to the Sion sub-region (bottom). Values above 0 indicate low competitive ability of oaks, whereas values below 0 indicate low competitive ability of pines.

mainly favored the pioneer species pine, have decreased strongly over the 20th Century, and these forests are now developing towards a later successional state, where pine as a light-demanding species is particularly subject to increasing intra- and interspecific competition for light. The patterns of both the competitive dynamics (Fig. 4) and the bai growth of pine (Fig. 5) illustrate that some pines have already entered the phase of increasing light competition and very slow growth, which may finally lead to higher mortality (Bigler et al., 2006). This case study of Valais thus illustrates how a changed disturbance regime results in altered successional patterns and stand structures (Linder et al., 1997).

Parallel to land-use changes, climatic changes also affect the growth and survival of these two tree species in Valais (Rebetz and Dobbertin, 2004; Weber et al., in press). Based on the interval trend analysis (Fig. 7), pines appear to be subject to higher competition in dry years, whereas oaks face higher competition in moderate years. These opposing growth patterns can be explained by the different life history strategies of the coniferous, sub-boreal pine versus the deciduous, sub-Mediterranean oak (Weber et al., in press). Because of their perennial needles, pines react less flexibly to drought than oaks, which have short-lived leaves. Moreover, pines presumably

develop a shallower rooting system than oaks, which makes them more susceptible to drought (Waring, 1987). Also, the growth response of oak was found to indicate a better adaptive capacity to a changing climate (Weber et al., in press), which, in Valais, has been characterized by warmer conditions particularly since the 1980s (Rebetz and Dobbertin, 2004) and by a shift in the seasonality of moisture availability (Weber et al., in press).

In fact, in the climatically more extreme Visp sub-region, the difference curve of ascending intervals in the competitive dynamics of oaks and pines correlated more strongly with drought than in the more oceanic Sion sub-region (Fig. 7), thus supporting the view that the species-specific drought response plays an important role in modulating interspecific competition between oak and pine. In a future changing climate, the diverging effect of the species-specific drought response is likely to gain further importance.

4.3. Deriving competitive dynamics from tree-ring data

Static competition indices provide a powerful tool to analyse the competitive structure of a forest stand. These competition indices do, however, have considerable limitations (Burton, 1993). The retrospective dynamic competition index proposed in our study has some distinct advantages. First, besides the spatial component, it also contains a temporal component, and thus allows us to reconstruct competitive dynamics over time. Second, by looking at both the level and the trend in competitive dynamics, we were able to identify (1) trees with increasing competition, even though they are growing at a low competition level (groups pine2 and pine4), and (2) trees with constant competition, even though they are growing on a high competition level (groups oak3 and oak4 in Fig. 4). The latter demonstrates that competition can be “intense without being significant” (Burton, 1993).

Some problems inherent to the exploration of inter-tree competition remain, nevertheless, unsolved. Belowground effects on competitive dynamics are difficult to study and therefore scarcely understood. Disentangling aboveground (light) and belowground (water and nutrients) competition is only feasible in field studies under experimental conditions where the influencing factors can be separated from each other. Generating such conditions could be difficult in Valais because of the strong past anthropogenic disturbances that have led to the heterogeneous growth forms of the trees and probably have overridden all other influencing factors.

In our study, the bai values of pine and oak were assumed to have an equal effect on the bai growth of neighbouring trees, although morphology varies considerably between the two species. However, this approach was justifiable and even appropriate because the comparison of intraspecific (oak with oak competitors, pine with pine competitors) versus interspecific (oak with pine competitors, pine with oak competitors) static and dynamic indices failed to reveal any interspecific differences. Consequently, it appears that pine is outcompeted equally well by both its pine and oak neighbours. Unfortunately, we did not record leaf area or crown volume variables,

which would have enabled us to directly calibrate the competitive effect of pine versus that of oak. Specifying the species-specific influence is a well-known problem in multi-species studies (Biondi et al., 1992; Berger and Hildenbrandt, 2000; Uriarte et al., 2004).

In spite of these limitations, using the new dynamic competition indices allowed us to directly compare the competitive ability of young and old trees over the same time span, which is a considerable advantage over classic age-stratified growth analyses (e.g. Motta and Nola, 2001). For stratification, the statistical clustering of the cumulative retrospective dynamic indices offers an alternative in those cases where age-stratified growth analyses are not feasible, i.e. within uneven-aged and uneven-structured forest stands. With our statistically based approach, however, we were still able to reveal the major competitive patterns over time.

Moreover, the retrospective dynamic competition index developed here integrates more information than ring-width curves alone. This can be seen by comparing the groups of competitive dynamics obtained from the cluster analysis (Fig. 4) with the individual bai curves that were grouped according to the same clusters (Fig. 5). While the tree-ring series account for temporal variability only, dynamic competition indices combine a temporal and spatial element, so that the growth potential of the neighbourhood becomes relevant for predicting the competitive ability of a tree.

5. Conclusions

The new retrospective dynamic competition index proposed here allows us to detect the trend underlying current competition, whereas classic static competition indices can describe only the current level of competition. The application of the retrospective dynamic competition index is particularly suitable in the case of (1) uneven-aged and uneven-structured stands where age-stratification fails, (2) stands with heterogeneous tree growth forms due to other factors, e.g. mixtures of light-demanding and shade-tolerant species, and (3) stands with heterogeneous spatial patterns. Combining the new dynamic index with standard static indices seems promising as a way of analysing past and estimating future stand development. The bai-based dynamic index provides a method to trace competitive dynamics with a high temporal resolution without repeated assessments, which represents a major advance in forest dynamics analyses. The dynamic index allows us to identify whether and when outcompeting processes are likely to occur, which can help in disentangling effects of land-use and climate change.

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