



## Mind the gaps: Comparison of representative vs opportunistic assessment of tree regeneration in Central European beech forests

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### ABSTRACT

Tree regeneration (TR) in canopy gaps is a key process to understand how forest ecosystems might adapt to future environmental changes. Since successful TR is the result of a complex interplay of several stochastic events such as gap formation, seed production, ungulate pressure and diseases, some of the processes have been neglected or strongly reduced for model applications. Most empirical data on TR originate from (national) forest inventories based on statistically optimized designs for timber resource estimations and use geographically fixed permanent plots. Consequently, these representative samples record TR both in gaps as well as under closed canopy conditions. In this study, we compared TR in 63 representative plots of the Swiss National Forest Inventory ('NFI sampling'), located in beech and silver fir-beech forests along an elevation gradient in the Jura Mts., with an opportunistic 'gap sampling' strategy targeting TR-clusters. We analyzed quantitative (e.g., number of individuals) and qualitative (e.g., species diversity, similarity to surrounding canopy) differences between the 'NFI sampling' and 'gap sampling,' as well as the environmental factors (e.g., gap size, cluster age, elevation) influencing the composition of TR in small canopy gaps. The 'gap sampling' recorded higher median TR densities (+62%, stems ha<sup>-1</sup>) and species richness ( $4.0 \pm 2.1$ , mean  $\pm$  sd) than the 'NFI sampling'. More importantly, the 'gap sampling' provided much more consistent results among sites (i.e., 4x lower variance). Consequently, the 'gap sampling' revealed not only general but also species-specific patterns across TR size classes and along elevational gradients in contrast to the lack of patterns in the 'NFI sampling'. Species richness decreased as TR grew taller, and the tallest TR size class (>130 cm) was almost solely comprised of the dominant species in the surrounding canopy (direct ingrowth). The high amount of direct ingrowth in TR indicates that small canopy gaps might offer only limited management potential to alter forests and that extensive disturbances or management at early TR stages (sapling) would be necessary to promote species better suited to the expected future site conditions. We raise the question of whether a forest monitoring that is statistically optimized for timber resource estimation is best suited to detect adaptation effects to quickly changing environments best visible at the regeneration stage, or whether forest inventory tools should be extended by methods that focus on disturbed parts of forests where changes and adaptations take place. We propose the implementation of an opportunistic gap-based monitoring of TR that essentially serves to identify the best forest management strategies (e.g. gap size, intervention intervals) in forests adapting to environmental change.

### 1. Introduction

Within a tree's life cycle, average environmental conditions and

frequencies of extreme events are expected to be drastically altered by climate change (IPCC 2019). A lack of resilience and resistance of forest ecosystems (Lindner et al. 2010; Jandl et al. 2019) to these changes

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might pose a risk for essential ecosystem services (Hanewinkel et al. 2013). Disturbances are expected to increase in the coming decades (Seidl et al. 2017) and, despite their destructive potential, might act as potential catalysts that enable forests to adapt to climate change (e.g., Thom, Rammer & Seidl 2017; Brice et al. 2020; Dietz et al. 2020; Scherrer et al. 2021). Because the elements of disturbance (e.g., agent, severity, frequency, extension and grain) are heterogeneously distributed in space and time, the analysis of disturbance impacts on forest adaptation is challenging and calls for representative field data (Seidl et al. 2011).

Disturbances (by natural events or by management) are spatially and temporally discrete events that disruptively change the resource availability and/or physical environment of forests (Pickett & White 1985), and are often associated with canopy openings. In canopy gaps, light availability is drastically increased, accelerating the establishment of a new tree generation (i.e., natural recruitment; Grubb 1977). While diverse factors such as the size of the gap, the topographic location (e.g., slope, aspect) or height of surrounding trees affect the regeneration in gaps (White & Jentsch 2001), tree regeneration in canopy openings is generally more rich in tree species than it is under a closed canopy (Muscolo et al. 2014; Zhu, Lu & Zhang 2014). Studies have shown that light-demanding species do not profit from canopy gaps smaller than 0.3 ha, while shade-tolerant species shoot up even in gaps of 0.05 ha (Malcolm, Mason & Clarke 2001; Webster & Lorimer 2005), leading to the expectation that small gaps are unlikely to change forest trajectories (Klopčič, Simončič & Bončina 2015).

In this study, we focus on European beech (*Fagus sylvatica*) forests that have experienced mostly small-scale natural disturbances, with the vast majority of canopy gaps being <0.05 ha (Schütz et al. 2016), and those which have been managed mostly close-to-nature (Johann 2006), enhancing natural tree regeneration by creating gaps of 0.05–0.5 ha (Schütz 1999; Brang et al. 2014). Close-to-nature silviculture aims to create diverse forest communities and thereby limit the stand-mortality risk and support adaptation to environmental changes (Brang et al. 2014; Allgaier Leuch, Streit & Brang 2017). However, whether close-to-nature silviculture alone facilitates forest transition under climate change is debated, as field observations often indicate direct regrowth (Spathelf, Bolte & van der Maaten 2015; O'Hara 2016; Kern et al. 2017) and forest transitions have mostly been observed after large-scale disturbances (Kramer et al. 2014; Dietz et al. 2020).

Information on tree regeneration (TR) after canopy disturbance is therefore essential to monitor the adaptive potential of beech forests to climate change. However, representative data on gap regeneration are difficult and time consuming to collect. Particular data on TR stem either from local case studies (i.e., not necessary representative; e.g., Abd Latif & Blackburn 2010; Hytteborn et al., 2014; Wohlgemuth & Kramer 2015) or from statistically optimized national forest inventories (e.g., Klopčič, Simončič & Bončina 2015; Nikolova et al. 2019; Scherrer et al. 2021). While national forest inventories provide representative information, they are usually optimized for timber resource estimation and record TR based on a fixed placement protocol (e.g., satellite plots). Consequently, TR is largely recorded under closed canopy and only to a small extent in gaps. This allows statistical estimations of the frequency of gaps, but only incompletely reflects the regeneration potential of sites in case of a disturbance event, a key process in determining future forest structure. This raises the question of whether the estimation of tree species composition and stem abundance differs between statistically representative TR assessments (e.g., national forest inventories) and opportunistic, gap-based surveys. Answers to this question have potential implications for the projection of the adaptive potential of forests in the context of climate change.

We used sample plot data from the representative Swiss National Forest Inventory (NFI, 'NFI sampling') in combination with a gap-oriented, opportunistic sampling ('gap sampling') of the same sites in mesophilic beech forests across the Jura Mts. in Switzerland to answer the following questions: (1) Do 'NFI sampling' and 'gap sampling'

provide different results regarding TR densities, tree species diversity and similarity with tree species composition of the surrounding canopy? (2) Which main factors determine TR densities, tree species diversity and similarity with surrounding canopy in small canopy gaps (climate vs dominant canopy species)? (3) To which degree does TR in small canopy gaps represent ingrowth of dominant canopy tree species indicated by high similarity or represent deviant forest trajectories?

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the Swiss Jura mountain chain from Nyon (46.43° E 6.07°) to Aarau (N 47.43° E 8.05°) covering an elevation gradient from 450 to 1440 m a.s.l. and encompassing an area of 3000 km<sup>2</sup> (Fig. 1). The bedrock consists mostly of limestone, marls and anhydrites, resulting in alkaline soils with high permeability (Frehner et al. 2009). At lower elevations the climate is oceanic warm-temperate (Cfb in Köppen-Geiger-Classification), transitioning towards a continental-wet climate at higher elevations (Dfb/Dfc in Köppen-Geiger-Classification; Beck et al. 2018), with annual precipitation sums around 1500 mm. Along the elevation gradient, three major vegetation belts can be distinguished: submontane (350–700 m a.s.l.) and lower montane (600–1000 m a.s.l.) forests dominated by beech and upper montane (900–1400 m a.s.l.) forests dominated by silver fir and beech (Fig. 1; Frehner et al. 2009). About 90% of the forest in the study area is managed, predominantly by a close-to-nature silviculture philosophy (Spathelf 1997; Pommerening & Murphy 2004) with small-scale interventions and long intervention intervals (Brändli, Abegg & Allgaier Leuch 2020).

### 2.2. Regeneration assessment in NFI plots and in canopy gaps

The fourth Swiss National Forest Inventory (NFI4) was conducted 2009–2017 over a 1.4 km × 1.4 km systematic permanent sample grid covering the whole country (Brändli & Hägeli 2019). In each NFI plot, standing and lying trees were measured using two concentric circular plots (500 m<sup>2</sup> and 200 m<sup>2</sup>). In the large plot all trees with a diameter at breast height (DBH) ≥ 36 cm were measured, while in the small plot trees and shrubs with a DBH ≥ 12 cm and < 36 cm were measured (Brändli & Hägeli 2019). Tree regeneration was assessed in a satellite plot located 10 m west of the NFI plot center, where stem numbers were recorded in concentric circles with  $r = 0.9$  m for heights 10–40 cm,  $r = 1.5$  m for heights of 40–130 cm,  $r = 2.5$  m for heights > 130 cm and DBH < 4 cm and  $r = 5$  m for DBH 4–8 cm (size classes; Düggelein & Keller 2017; Brändli & Hägeli 2019). From all the available NFI data, we extracted the canopy height (m), crown cover in canopy layer (%), 50 m × 50 m area), species contribution to TR (%) and TR density per species (TR<sub>ρ<sub>taxa</sub></sub>; upscaled to stems ha<sup>-1</sup>).

For the purpose of our study, we selected 21 NFI plots in each vegetation belt (63 out of 419 available NFI plots in the Jura Mts.; Fig. 1) based on the following criteria: plot is located within an area of one forest site type (i.e., either submontane beech forest, lower montane beech forest or upper montane silver fir-beech forest), contains no roads or forest edges and its canopy forming trees have a minimum age of about 30 years (i.e., > 20 m canopy height).

The selected 63 NFI plots were visited in summer 2019 (14th June–31st July 2019). In each NFI plot, the interpretation area (50 m × 50 m) was screened for canopy gaps and associated clusters of tree regeneration (hereafter called 'gaps'). The center of each gap was defined as the center of mass of the three tallest individuals, and the gap area was approximated by measuring the TR-cluster as an ellipse (Fig. 2). The TR (number of stems) in each gap was estimated within a circle around the center ( $r = 4$  m) and the counting/classification method was identical to the NFI4 (Düggelein & Keller 2017). A gap was excluded from the analysis if the center was outside of the interpretation

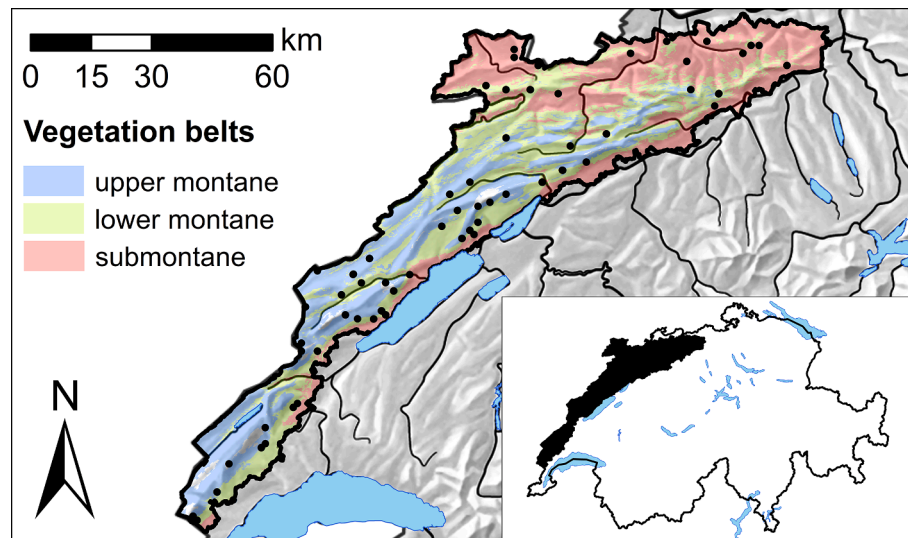


Fig. 1. Study area with the selected NFI plots (black dots) and the three main vegetation belts of the Jura Mountains (color shades).

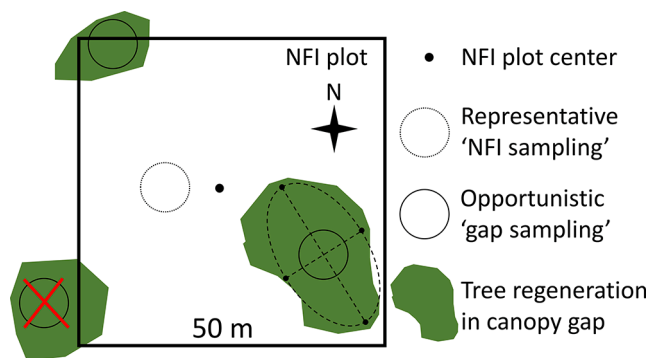


Fig. 2. Example of the representative ‘NFI sampling’ and opportunistic ‘gap sampling’ at an imaginary NFI plot.

area, if the gap was smaller 50 m<sup>2</sup>, if the height of the TR was >8 m (age about 7–10 years; Wohlgenuth & Kramer 2015) or if there were signs of silvicultural manipulation (i.e., species regulation by foresters; Fig. 2). In rare cases ( $N = 4$ ) where the entire interpretation area was very open and showed uniform TR, two plots (12.5 m north and south of the NFI plot center) were selected.

Out of all the tree species observed in the TR and canopy layer, only a few dominated our sites. We therefore regrouped the species into eight simplified taxa: *Abies alba* (silver fir), *Picea abies* (Norway spruce), *Fagus sylvatica* (European beech), *Fraxinus excelsior* (European ash), *Acer* spp. (maple), *Quercus* spp. (oak), *Sorbus* spp. (e.g., whitebeam, rowan) and ‘other spp.’ (see Table S1 for details on classification).

### 2.3. Statistical analysis

For each NFI plot, the data of all ‘gaps’ (if more than one was present within an NFI plot) were pooled and TR density ( $TR\rho$ ; stems ha<sup>-1</sup>) for each size class and species was calculated to allow direct comparison with NFI data.

For both ‘NFI sampling’ and ‘gap sampling’ we calculated species richness (SR) and the Simpson Diversity index ( $D$ ; Simpson 1949) of TR per NFI plot. For each NFI plot we also calculated the Bray-Curtis similarity (using percentage contribution as abundance; BC; Bray & Curtis 1957) and Sørensen similarity (presence/absence of species;  $S$ ; Sørensen 1948) between TR and the surrounding canopy (50 m × 50 m interpretation area) as well as direct ingrowth, being the percentage of TR

consisting of species present in the canopy layer. Cases where the ‘NFI sampling’ did not record any TR (i.e., no stems within the satellite plot) were removed from analysis of diversity and similarity, as these metrics cannot be calculated in such cases.

Preliminary analysis revealed that  $TR\rho$  both in the ‘NFI samples’ and ‘gap samples’ were strongly positively skewed (i.e., many small values and few very large ones; Figure S1); the data was therefore transformed (cubic root) to approximate normal distribution. Post-transformation normality was assessed by qqplot analysis and Shapiro-test (Shapiro & Wilk 1965). Potential differences in variance of  $TR\rho$  among sites between ‘NFI samples’ and ‘gap samples’ were assessed by a Brown–Forsythe Levene-type procedure (Brown & Forsythe 1974) using the function ‘levene.test’ from the ‘lawstat package’ (Gastwirth et al. 2020) in ‘R 4.0.1’ (R Core Team 2020). In cases where the data were approximately normally distributed but showed variance heterogeneity, Welch-t-tests (Welch 1947) were used to compare different groups (e.g., representative vs gap, different size classes or vegetation belts). In cases of non-normal distributions (even after transformation) but homogeneous variances among groups, non-parametric Wilcoxon-Rank-Sum tests were employed. A Holm correction (Holm 1979) was used to adjust p-values in cases of multiple pairwise comparisons.

A multi-model-inference approach was used to assess the influence of environmental factors on TR densities ( $TR\rho$ ), diversity ( $SR_G$ ,  $D_G$ ), similarity to the surrounding canopy ( $BC_{G-C}$ ,  $S_{G-C}$ ,  $DI_{G-C}$ ) as well as the TR density of key species ( $TR\rho_{\text{taxa}}$ ). The gap ratio ( $G_{\text{ratio}}$ ; gap area standardized by canopy height), maximum height of TR-cluster ( $G_{\text{height}}$ ; proxy for gap age), canopy diversity ( $SR_C$ ,  $D_C$ ) elevation a.s.l. (Ele; proxy for climate), slope, northernness and (for the  $TR\rho_{\text{taxa}}$  models only) proportional contribution of species to the canopy layer ( $C\%_{\text{taxa}}$ ) were used as potential predictors (see Table 1 for details on predictors and response variables). Global models included all the potential predictors as linear terms with all possible 2-fold interactions. We did not use quadratic terms in our models, as the spanned gradients (e.g., elevation) were too small to expect unimodal responses. All potential candidate models were evaluated based on Akaike information criterion for small sample sizes ( $AIC_c$ ), and the best models ( $\Delta AIC_c < 2$ ) were averaged to determine predictor influence and weighted variable importance. We used linear models (Gaussian) or generalized linear models (GLM) if the response variable was Poisson distributed (i.e.,  $SR_G$ ). All multi-model-inference analyses were carried out in ‘R 4.0.1’ (R Core Team 2020) using the ‘MuMIn package’ (Barton 2020).

**Table 1**  
Response variables and predictors used for the analyses and modelling.

Symbol	Type	Description	Unit
TR <sub>ρ</sub>	Response	Tree regeneration density per ha	stems ha <sup>-1</sup>
TR <sub>ρ<sub>taxa</sub></sub>	Response	Tree regeneration density per ha of a specific taxa	stems ha <sup>-1</sup>
SR <sub>G</sub>	Response	Species richness of tree regeneration	–
D <sub>G</sub>	Response	Simpson diversity index in tree regeneration (Simpson 1949)	–
BC <sub>G-C</sub>	Response	Bray-Curtis similarity between tree regeneration and surrounding canopy on the NFI-plot (Bray & Curtis 1957)	–
S <sub>G-C</sub>	Response	Sørensen similarity between tree regeneration and surrounding canopy on the NFI-plot (Sørensen 1948)	–
DI <sub>G-C</sub>	Response	Direct ingrowth in tree regeneration as percentage contribution by species found in the surrounding canopy on the NFI-plot	%
G <sub>ratio</sub>	Predictor	Ratio of the canopy height to the shorter of the two ellipse axes of the tree regeneration cluster	–
G <sub>height</sub>	Predictor	Average height of the three tallest individuals in the tree regeneration cluster (approximation for gap age)	m
D <sub>C</sub>	Predictor	Simpson diversity index of the surrounding canopy layer on the NFI-plot	–
Ele	Predictor	Elevation above sea level (proxy for climate)	m
Slope	Predictor	Slope of the site calculated based on a digital elevation model (25 m resolution)	–
North	Predictor	Aspect, calculated based on a digital elevation model (25 m resolution) and transformed into northerness [cos(aspect)]	–
C% <sub>taxa</sub>	Predictor	Proportion of a certain taxa in the surrounding canopy layer on the NFI-plot	%

### 3. Results

In total across our 63 NFI plots, we recorded 124 TR-clusters in canopy gaps, of which 38 were located in the submontane, 44 in the lower montane and 42 in the upper montane vegetation belt. The mean gap area was  $136 \pm 102 \text{ m}^2$  (mean  $\pm$  sd) and the average gap height (i.e., average of the three most mature individuals) was  $3.8 \pm 1.8 \text{ m}$  (Figure S2). The majority of our plots were south or southeast facing and showed a slope ranging from 0 to  $30^\circ$  (Figure S3).

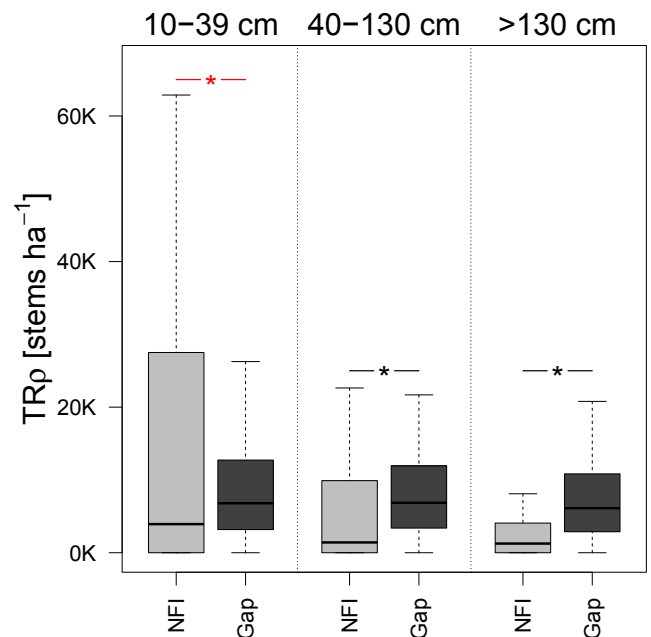
#### 3.1. NFI vs gap sampling of tree regeneration

##### 3.1.1. Tree regeneration density

TR<sub>ρ</sub> (stems ha<sup>-1</sup>) in the 'NFI samples' was significantly lower ( $p < 0.01$ ; Welch-*t*-test) and expressed higher variability ( $p < 0.01$ ; Brown-Forsythe-test) than in the 'gap samples' (Figure S4). This difference in variance was mostly driven by the lowest TR size class (10–40 cm), as the taller TR (40–130 cm and  $> 130 \text{ cm}$ ) showed no significant difference in variance but a significant difference in mean TR<sub>ρ</sub> (Fig. 3). The 'NFI sampling' showed no significant differences in TR<sub>ρ</sub> across vegetation belts while the 'gap sampling' revealed decreasing TR<sub>ρ</sub> along elevation (Figure S5).

##### 3.1.2. Tree regeneration diversity

Overall species richness and Simpson diversity index were higher in 'gap samples' compared to the 'NFI samples' ( $p < 0.01$ , Welch-*t*-test; Figure S6). In 'NFI samples,' both species richness and Simpson diversity did not change across TR size classes, while in the 'gap samples' they both significantly decreased with increasing TR age/size classes (Figure S7). Species richness in 'gap samples' was higher than in 'NFI samples' for all TR size classes and vegetation belts. The Simpson diversity index in gaps was significantly higher only in the submontane and lower montane beech forests and for TR  $< 130 \text{ cm}$  (Fig. 4).



**Fig. 3.** Tree regeneration density (TR<sub>ρ</sub>; stems ha<sup>-1</sup>) estimated across the 63 NFI plots based on the 'NFI sampling' and 'gap sampling' separated into the three size classes. The black and red asterisks indicate significant differences in mean ( $p < 0.05$ ; Wilcoxon Rank-sum-test) and variance ( $p < 0.01$ ; Brown-Forsythe-test), respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

##### 3.1.3. Tree regeneration similarity to surrounding canopy

TR in 'gap samples' showed a higher Bray-Curtis similarity ( $p < 0.01$ ; Wilcoxon rank-sum-test) with the surrounding canopy than TR in 'NFI samples,' while there was no difference in Sørensen similarity or direct ingrowth (Figure S8). The amount of direct ingrowth significantly increased towards the taller TR size classes in our 'gap samples,' while the same trend was not significant in the 'NFI samples' (Fig. 5), indicating that taller TR almost solely consists of species present in the surrounding canopy.

##### 3.1.4. Taxa-specific patterns

TR was mostly dominated by broadleaf species, but the proportion of conifer species increased with elevation (Fig. 6). The lowest TR (10–40 cm) was most diverse and showed the most even distribution of taxa (i. e., several taxa with similar stem numbers), while the tallest TR ( $> 130 \text{ cm}$ ) resembled mostly the dominant tree species (one or two) in the canopy. Regarding specific taxa, our data show that the TR densities of *P. abies* and *Sorbus* spp. in gaps increase with elevation while the densities of *F. excelsior*, *Quercus* spp. and other spp. decrease (Figure S9). *Fagus sylvatica* was the only species that showed an increased abundance in the taller TR size classes, while all other species showed a reduced or stable density in taller TR (Figure S10). None of these patterns were obvious in the 'NFI sampling'. More importantly, all species except *F. sylvatica* showed no persistent presence in the 'NFI sampling' and were mostly missing from  $> 50\%$  of the plots (Figure S10).

#### 3.2. Determinants of tree regeneration in small canopy gaps

TR density in small canopy gaps was significantly increasing with gap size (G<sub>ratio</sub>), decreasing with elevation and gap height (G<sub>height</sub>; proxy for gap age) and showed a positive interaction with G<sub>ratio</sub> and slope ( $R^2 = 0.35$ ; Table 2a). The species richness of gaps (SR<sub>G</sub>) was not significantly influenced by any predictor, but variable importance indicated decreasing SR<sub>G</sub> with G<sub>height</sub> ( $R^2 = 0.17$ ; Table 2a). The Simpson diversity of gaps (D<sub>G</sub>) was hardly affected by any predictors, but showed a

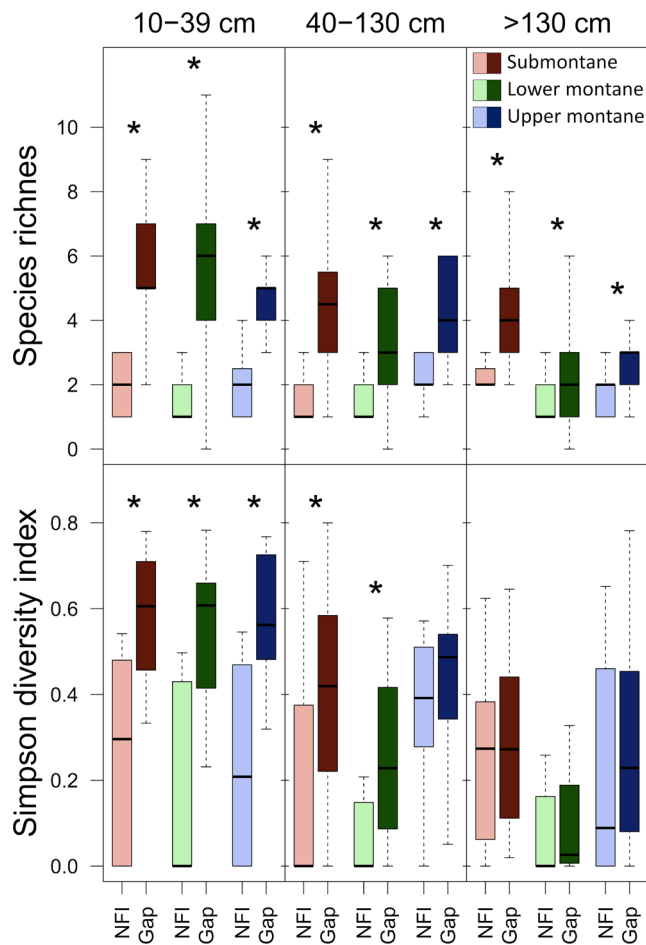


Fig. 4. Tree regeneration diversity expressed as species richness and Simpson diversity index in the 21 NFI plots per vegetation belt based on 'NFI sampling' and 'gap sampling' for different size classes (columns). Asterisks indicate significant differences between the two sampling strategies ( $p < 0.05$ , Wilcoxon rank-sum-test).

significant increase with  $G_{ratio}$  and a positive interaction with  $G_{ratio}$  and slope ( $R^2 = 0.14$ ; Table 2a). Bray-Curtis similarity between gaps and the surrounding canopy ( $BC_{G-C}$ ) significantly decreased with elevation and canopy Simpson diversity ( $D_C$ ), and showed a number of significant interactions among predictors ( $R^2 = 0.31$ ; Table 2a). Sørensen similarity between gaps and the surrounding canopy ( $S_{G-C}$ ) seemed to increase with  $G_{height}$  and to decrease with elevation and  $D_C$  ( $R^2 = 0.37$ , Table 2a). Direct ingrowth ( $DI_{G-C}$ ) decreased with elevation and  $D_C$  and increased with northerness ( $R^2 = 0.32$ , Table 2a).

The TR density of *A. alba* ( $TR_{\rho A. alba}$ ) was positively influenced by the proportion of *A. alba* in the surrounding canopy and northerness, as well as number of interactions with elevation ( $R^2 = 0.39$ ; Table 2b). *Picea abies* density ( $TR_{\rho P. abies}$ ) was positively influenced by the proportion of *P. abies* in the surrounding canopy and elevation ( $R^2 = 0.56$ , Table 2b). *Fagus sylvatica* mostly profited from larger canopy openings ( $G_{ratio}$ ) and was more dominant on north facing slopes ( $R^2 = 0.42$ ; Table 2b). *Fraxinus excelsior* was mostly present at lower elevations ( $R^2 = 0.38$ ; Table 2b). The explanatory power of the models for *Acer* spp. was low, but the species significantly decreased with elevation and increased with northerness ( $R^2 = 0.15$ , Table 2b). *Quercus* spp. were mainly present in younger canopy gaps ( $G_{height}$ ) and at low elevation but showed complex interactions with predictors as well ( $R^2 = 0.76$ , Table 2b). *Sorbus* spp. were significantly more prominent in gaps at higher elevations and on steeper slopes ( $R^2 = 0.45$ , Table 2b).

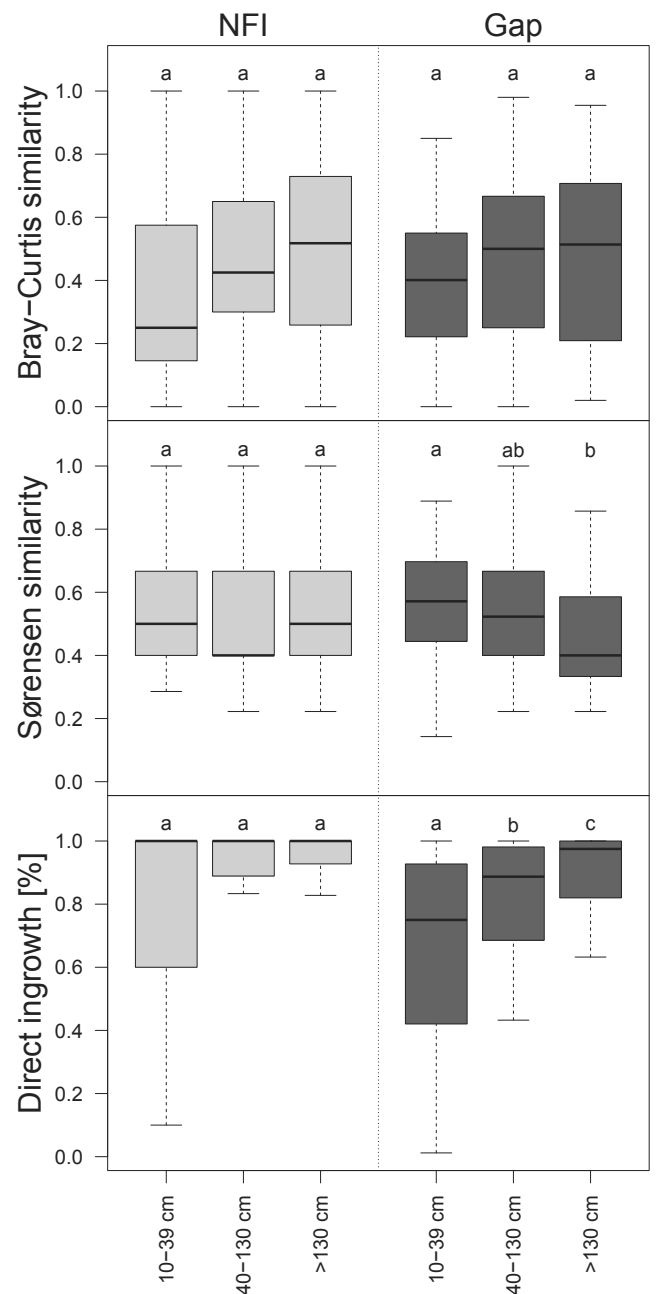
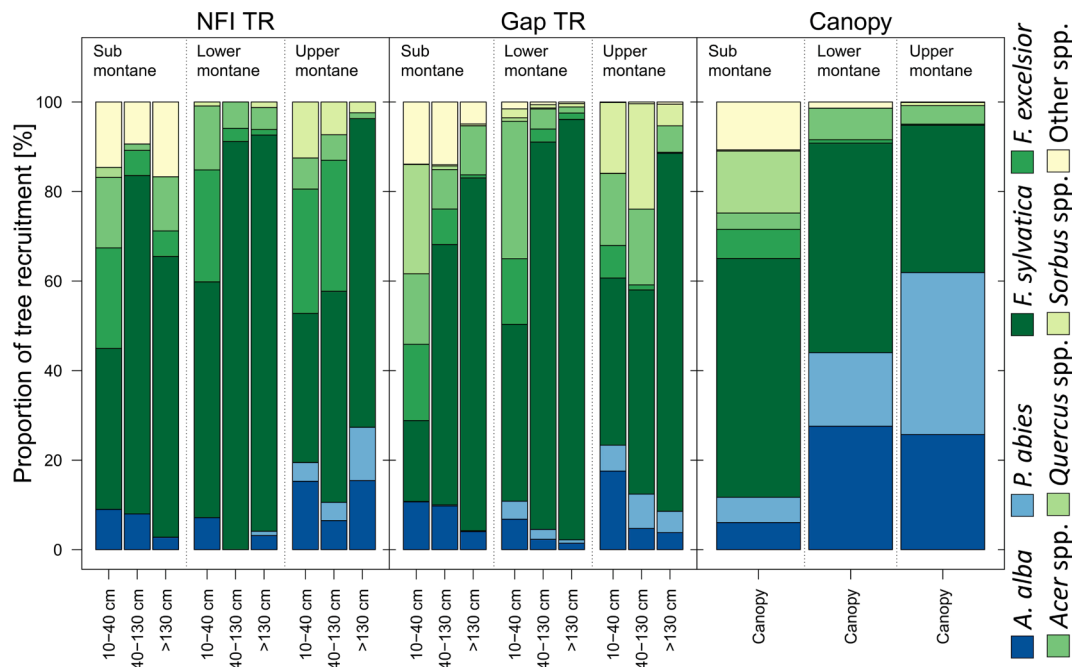


Fig. 5. Bray-Curtis similarity, Sørensen similarity and direct ingrowth between either 'NFI samples' or 'gap samples' with the surrounding canopy layer of the 50 m × 50 m interpretation area separated into three size classes. Letters indicate significant differences in mean values across size classes ( $p < 0.01$ ; pairwise-Wilcoxon test with Holm correction).

#### 4. Discussion

The opportunistic 'gap sampling' recorded higher TR densities than the representative 'NFI sampling,' which returns TR to a great extent under closed canopy and results in considerably larger variance of TR densities. Aside from the differences in variance of TR density, several regeneration characteristics in tree size classes and between vegetation belts emerged from 'gap sampling' (e.g., reduction of biodiversity, increase in direct ingrowth and decreasing similarity with canopy cover), but not from the 'NFI sampling'. The size distribution in the canopy gaps was in line with gaps recorded in primeval beech forests in Eastern Europe (Hobi et al. 2015), indicating that our findings from the 'gap sampling' might be, to some extent, generalizable for European beech



**Fig. 6.** Proportional contribution of different tree taxa to TR in 'NFI samples,' TR in 'gap samples' and surrounding canopy layer of the 50 m × 50 m interpretation area. Data is separated by vegetation belt (submontane, lower montane and upper montane) and for the TR by size class (10–40 cm, 40–130 cm, >130 cm). For details on taxa see Table S1.

forests.

#### 4.1. Representative vs opportunistic sampling of tree regeneration

National forest inventories mainly serve the purpose of monitoring the structure and growth of forests, and in particular timber resources (Brändli et al. 2020). As a side effect of the statistically optimized design of most NFI and a general systematic assessment, plots inside of gaps are rare, resulting in sparse information on gap regeneration. Given the universal importance of the realized regeneration niche in gaps, the typical information of forest inventories on regeneration mainly reports on the variant of tree regeneration under canopy, which consist of few highly shade-tolerant species (Grubb 1977; Savage, Brown & Feddema 1996). We therefore expected our opportunistic 'gap samples' to show higher average TR densities than the representative 'NFI samples,' though no significant differences were observed for the lowest and most abundant TR size class (10–40 cm). Our data suggest this to be an artefact of differences in circle plot sizes rather than sampling strategies (i.e., representative vs opportunistic). In the 'NFI sampling,' the lowest TR size class (10–40 cm) was recorded in a plot circle with  $r = 0.9$  m (compared to  $r = 4$  m in opportunistic sampling), leading to larger upscaling uncertainty and consequently significantly different variances. This strong influence of the circle plot sizes was further highlighted by the fact that in the taller TR size class (40–130 cm and >130 cm; with comparable circle plot sizes) there was no difference in variance but significantly higher numbers in mean TR densities.

Tree regeneration diversity (species richness and Simpson diversity) was consistently higher in our 'gap samples,' especially in the lowest TR size classes, and decreased towards tallest TR size classes. The species lost during this selection process were mostly "external" species, i.e. species not represented in the surrounding canopy. In agreement with this finding, direct ingrowth increased across TR size classes. This indicates that tree species originating from outside of the 50 m × 50 m interpretation area eventually fail to survive in taller size classes, while individuals of the dominating canopy species eventually prevail the sapling stage. The majority of the gaps we found were probably too small ( $136 \pm 102$  m<sup>2</sup>) for the spread and rise of light-demanding tree

species in competition with the shade-tolerant species typically persisting under closed canopy (e.g., Malcolm, Mason & Clarke 2001; Webster & Lorimer 2005).

Overall, both the 'NFI sampling' and 'gap sampling' found that TR mostly represents direct ingrowth of the dominant tree species. Many tree species in forests regenerate in pulses realized in canopy gaps (Zackrisson et al. 1995; Jentsch & White 2019), and only the most shade-tolerant species – among which is beech – are able to build up an abundant 'seedling bank' under closed canopy (Grubb 1977; Savage, Brown & Feddema 1996). In a small gap, the window of opportunity for seedling establishment for new species lasts only for a short time, and most gaps will be filled with seedlings from the already present, dominant species (Moser et al. 2010; Maringer et al. 2020). In the small gaps assessed in the studied beech forests, the dominating tree species drove species selection, and no shifts in vegetation trajectories were detected. The structurally caused persistence of canopy trees by natural regeneration contrasts with other studies that consider larger-scale disturbances such as patch-forming windthrow, insect outbreaks or drought-induced mortality as events that might shift vegetation trajectories towards either climatically 'better-adapted' species (e.g., Allen, Breshears & McDowell 2015; Batllori et al. 2020; McDowell et al. 2020; Scherrer et al. 2021) or earlier succession stages (pioneer forests; Rigling et al. 2013; Wohlgemuth et al. 2018). In these cases, the expectations based on representative and opportunistic sampling might be substantially different, as the representative data seems to underestimate post-disturbance development potential of TR (e.g., species diversity). Tree regeneration data based on representative sampling might suffer from the large uncertainties that often result from analyses simply based on presence/absence of species rather than quantitative data (Wohlgemuth, Gallien & Zimmermann 2016; Kolo, Ankerst & Knoke 2017). This might be problematic, since the representative data only poorly reflects TR in gaps, where the adaptive potential of forests to changing environmental conditions would be first and most detectible (White & Jentsch 2001; Körner et al. 2016; Scherrer et al. 2021). In recent years, evidence has grown that several currently dominant tree species might be at risk due to ongoing climate change (e.g. prolonged drought periods for Beech; Schuldt et al. 2020), insect attacks (e.g., bark beetle in spruce;

**Table 2**Summary of model performance and weighted variable importance based on multi-model-inference and model averaging of all models  $\Delta AICc < 2$ .

(a) Results for model on TR density (TR $\rho$ ), diversity (SR $_G$ , D $_G$ ) and similarity to canopy layer (BC $_{G-C}$ , S $_{G-C}$ , DI $_{G-C}$ ).														
Response	Model performance		Weighted variable importance (Main factors)						Weighted variable importance (Interactions)					
	pR <sup>2</sup>	N	G <sub>ratio</sub>	G <sub>height</sub>	Ele	D <sub>c</sub>	Slope	North	G <sub>ratio</sub> : Slope	Ele: D <sub>c</sub>	Ele: North	D <sub>c</sub> : North	Slope: North	
TR $\rho$	0.35	15	+1*	-1*	-1*	+0.17	-0.87	-0.51	+0.75*	-	-	-	+0.18	
SR $_G$	0.17	16	+0.49	-1	-0.76	-0.66	+0.05	-	-	-	-	-	-	
D $_G$	0.14	13	+0.45*	-	+0.33	-0.91	-1	+0.78	-0.45*	-0.11	-0.15	+0.06	-0.49	
BC $_{G-C}$	0.31	5	+0.17	-0.69	-1*	-1*	-1	+1	+0.69*	+1*	+1*	-1*	-0.83*	
S $_{G-C}$	0.37	8	-	+1	-1	-1	-0.56	-	-	+1*	-	-	-	
DI $_{G-C}$	0.32	5	+0.17	+0.2	-1*	-1*	+1	+1*	-	+1*	+0.14	-1*	-	

(b) Results for models on TR densities of individual key taxa. Variables with significant effects that were selected in all models are highlighted in colour, with red for negative and green for positive influence.																		
Response	Model performance		Weighted variable importance (Main factors)						Weighted variable importance (Interactions)									
	pR <sup>2</sup>	N	G <sub>ratio</sub>	G <sub>height</sub>	Ele	C% <sub>taxa</sub>	Slope	North	G <sub>ratio</sub> : Ele	G <sub>ratio</sub> : C% <sub>taxa</sub>	G <sub>ratio</sub> : North	G <sub>height</sub> : C% <sub>taxa</sub>	Ele: C% <sub>taxa</sub>	Ele: Slope	Ele: North	C% <sub>taxa</sub> : Slope	C% <sub>taxa</sub> : North	Slope: North
TR $\rho_{A. alba}$	0.39	3	-1	-	-1	+1*	+1	+1*	+1*	+0.17	-	-	-1*	-0.61	-1*	-1*	-	-
TR $\rho_{P. abies}$	0.56	7	+1	+0.08	+1*	+1*	+1	+1	+0.4	-	-	+0.08	-0.19	-1*	+0.64	-	-	-
TR $\rho_{F. sylvatica}$	0.42	13	+1*	-1	+1	-1	+1*	-1	-0.42	+0.11	-1*	+0.05	+1*	-1*	-0.39	-1*	-	+1*
TR $\rho_{F. excelsior}$	0.38	7	-0.12	-0.11	-1*	-0.85	-1	-0.11	-	-	-	-	+0.14	+1*	-	-	-	-
TR $\rho_{Acer spp.}$	0.15	8	-0.19	-0.1	-1*	-1	+0.3	+1*	-	-	-	-	+0.53	-	-1*	-0.11	-1*	-
TR $\rho_{Quercus spp.}$	0.76	10	+0.74	-1	-1*	-1*	-1	-0.09	-0.14	-0.74*	-	+1*	+1*	+0.72	-	-1*	-	-
TR $\rho_{Sorbus spp.}$	0.45	12	+0.34	+1	+1*	0.29	+1*	-0.61*	-	-	-	-	-	-1*	-	-	-	+0.61

Asterisks mark significant influences in the average model ( $p < 0.05$ ). Interactions that never showed any significant effect were removed from the table. For details on taxa see Table S1. For details on response variables and predictors see Table 1.

pR<sup>2</sup> = pseudo R<sup>2</sup> of average model.

N = Number of models selected for averaging ( $\Delta AICc < 2$ ).

Stadelmann et al. 2014) and diseases (e.g., Ash dieback; Hill et al. 2019). Therefore, the question is raised if certain forests could and should be actively transformed away from the currently dominant species towards new species mixtures to prevent potential future loss of important ecosystem functions (Lindner et al. 2014). In that respect, our results indicate that small canopy gaps provide little management potential to transform forests, and imply that patch-size disturbances or management interventions (e.g., 1 or several hectares) might represent better windows of opportunity for both natural regeneration processes as well as silvicultural measures.

#### 4.2. Determinants of tree regeneration in small canopy gaps

Larger gaps ( $G_{\text{area}}$  and  $G_{\text{ratio}}$ ) showed higher TR densities and species richness. This relationship was observed in several studies (Muscolo et al. 2014; Zhu, Lu & Zhang 2014) and generally reflects a species-area relationship. In our case, however, the sampling area was identical ( $r = 4$  m), independent of gap size. The increase in density and species richness of gaps, therefore, is most likely an effect of increasing resource availability (in particular light and temperature) in larger gaps, allowing the establishment of all tree species, especially the more light-demanding ones, and supporting higher densities of individuals. Both TR densities and species richness decreased with gap age and TR size class as a result of self-differentiation resulting from competition for resources, which is in line with observations in the beech forests of Eastern Europe (Klopčič, Simončič & Bončina 2015). In our case, this competitive exclusion process seemed to favor species already dominant in the canopy layer (especially *F. sylvatica* and *A. alba*), leading to an increase in Sørensen index of tree species in gaps and canopy as well as direct ingrowth with increasing  $G_{\text{height}}$  and TR size classes. Given our rather small gap sizes ( $136 \pm 102$  m<sup>2</sup>), the increasing dominance of the more shade-tolerant climax species *F. sylvatica* and *A. alba* (Grubb 1977; Savage, Brown & Feddema 1996) is not surprising and in line with earlier findings in beech forests (Bončina 2000; Stancioiu & O'Hara 2006). Along the elevation gradient, TR density and TR diversity decreased significantly. The reduced TR diversity at higher elevation is mostly due to the elevational limits of broadleaf tree species (i.e., *F. excelsior*, *Quercus* spp. and 'other spp.' including *Carpinus betulus*, *Ilex aquifolium*, *Juglans regia*, *Tilia* spp. and *Prunus* spp.), while only *Sorbus* spp. showed a positive trend with elevation (in agreement with Randin et al. 2013) resulting in an overall loss of TR diversity. This dependency of TR density and diversity with elevation is in line with earlier findings (e.g. Wohlgemuth et al. 2008; Bachofen 2009; Wohlgemuth & Kramer 2015; Wohlgemuth et al. 2017) and many of the "lower elevation" taxa might reach the limit of their fundamental niche in the highest elevations of the Jura Mountains (Wohlgemuth, Gallien & Zimmermann 2016). The positive effect of elevation on the early successional *Sorbus* spp. (namely *S. aucuparia* and *S. aria*) was most likely linked to the increased light availability and reduced competition in the more open higher-elevation forests of the Jura Mts.

While the proportion of conifers in the canopy layer is considerably higher in upper montane vegetation belt of the Jura Mts, the TR still showed a high proportion of broadleaf species, especially *F. sylvatica* (about 80% in the TR > 130 cm). This might be an indication that *F. sylvatica* is expanding its range into higher elevations, profiting from warmer climatic conditions and lower frequencies of late spring frost events (Vitasse et al. 2012). However, several sites showed considerable browsing damage by deer, potentially suppressing conifers (especially *A. alba*; Kupferschmid, Brang & Bugmann 2019; Kupferschmid & Heiri 2019) and favoring the largely unaffected *F. sylvatica* saplings (Frank, Heiri & Kupferschmid 2019). Time will tell whether the observed high abundance of *F. sylvatica* in TR of the upper montane vegetation belt, traditionally dominated by *A. alba* and *P. abies* (Frehner et al. 2019), will eventually result in a vegetation shift towards beech forests or whether the majority of these *F. sylvatica* saplings will eventually be eliminated by management or die off at a later stage, e.g., once too tall to profit from

shelter of existing canopy (Lenoir et al. 2013; Lenoir, Hattab & Pierre 2016).

*Fagus sylvatica* generally dominated the TR in these different types of beech and silver fir-beech forests of the Jura Mts, which especially holds true for the taller TR size classes. This dominance is likely the result of a combination of the high prevalence of *F. sylvatica* in the canopy layer, leading to a dense seed load (Frank, Heiri & Kupferschmid 2019), and the high shade tolerance of beech seedlings, allowing their establishment even under closed canopy conditions (Niinemets & Valladares 2006). After canopy disturbance, already present seedlings of *F. sylvatica* outcompete more light-dependent species that usually start from seed brought by wind (Moser et al. 2010). The second stand-forming species *A. alba* was much less prevalent in tree regeneration despite its high TR potential (Dobrowolska, Bončina & Klumpp 2017) and, in line with other studies, seemed to prefer diffuse light conditions (i.e., smaller and older gaps on North-exposed slopes; Rozenberger et al. 2007). The TR success of *P. abies* was mostly dependent on the dominance of mother trees in the surrounding canopy and related pulse-wise seed rain. In the studied beech forests, *P. abies* seems unable to establish a permanent seedling bank (Berger & Walther 2006), depending rather on the seed mast of canopy trees (i.e., the dominance in the surrounding canopy). The high proportion of adult *P. abies* in these beech forests is a legacy of past forest management decisions in the frame of adopted German silvicultural systems (Bürgi & Schuler 2003), and several studies suggest that *P. abies* decrease in frequency after disturbance events in these beech forests (Kramer et al. 2014; Scherrer et al. 2021). As expected, many characteristic broadleaf species (i.e., *Quercus* spp., *F. excelsior* and Other spp.) were mainly present in the lowest vegetation belt and quickly decreased in frequency with elevation. Additionally, both *F. excelsior* and *Acer* spp. (predominantly *A. pseudoplatanus*) were abundantly present at most sites in the lowest TR size class but not so in later stages of TR. In small canopy gaps, *F. sylvatica* dominates over the less shade-tolerant *A. pseudoplatanus* as an effect of competitive exclusion, while *F. excelsior* loses competitive power as it suffers from ash dieback caused by *Hymenoscyphus fraxineus* (Marcais et al. 2017; Enderle, Stenlid & Vasaitis 2019).

#### 5. Conclusions

The aim of this study was to evaluate whether representative samples such as in the frame of national forest inventories are able to adequately reflect the post-disturbance regeneration potential in the small canopy gaps of beech forests. We demonstrated distinct differences in the quantity and the composition of TR assessed in canopy gaps vs assessed under canopy. Mixing these two coarse types of structural site conditions leads to high variation in TR density and diversity, which increases the projection uncertainty of TR (e.g., Madsen & Hahn 2008; Vacchiano et al. 2018; Jaloviar et al. 2020) and reduces the statistical power in quantitative analyses, potentially obscuring regeneration dynamics. This outcome is particularly relevant to the development of realistic recruitment projections under presumed increasing disturbance frequencies and severities in the face of ongoing climate change (Seidl et al. 2017). An opportunistic gap sampling (i.e., an assessment of multiple gaps) in addition and in close proximity to representative sampling plots, allows better accounting of the regeneration potential taking place in the realized niche (e.g., mast strategies; Allen, Millard & Richardson 2017; Nussbaumer et al. 2018; Bogdziewicz et al. 2020) and thereby provides a more consistent estimation of post-disturbance TR potential.

Our finding that the lowest TR classes showed high species diversity (including species not dominant in the surrounding canopy) while the tallest TR represented almost exclusively direct ingrowth of the dominant canopy species indicate that small canopy gaps might offer little potential for adaptive management to transform forests in the context of climate change. We question whether a forest monitoring scheme statistically optimized for timber resource estimation is best suited to monitor early responses to environmental change in order to anticipate



future development, and whether forest monitoring tools should integrate the observation of gap-related processes, as regeneration in gaps proceeds rapidly. We believe that an opportunistic gap-based monitoring of TR would be beneficial to surveying the adaptive potential of natural regeneration during climate change, beyond forest management strategies that use gap dynamics to derive specific measures for building future forests.

### CRedit authorship contribution statement

**Daniel Scherrer:** Methodology, Formal analysis, Investigation, Writing - original draft, Visualization, Supervision. **Fabien Hildebrand:** Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **Jürgen Dengler:** Writing - review & editing, Supervision. **Thomas Wohlgemuth:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119179>.

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