Tree Species Assemblages, Stand Structure, and Regeneration in an Old-Growth Mixed Conifer Forest in Kawang, Western Bhutan

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Abstract

Old-growth mixed-conifer forests in Bhutan are characterized by remarkable tree species compositional heterogeneity. However, our knowledge of tree species assemblages and their structural attributes in these forests has been limited. Therefore, forest classification has been reliant on a single dominant species. This study aimed to distinguish tree species assemblages in an old-growth mixed conifer forest in Western Bhutan and to describe their natural compositional and stand structural characteristics. Furthermore, the regeneration status of species was investigated and the quantity and quality of accumulated coarse woody debris were assessed. Ninety simple random sampling plots were surveyed in the study site between 3,000 and 3,600 meters above sea level. Tree, standing deadwood, regeneration, and coarse woody debris data were collected. Seven tree species assemblages were distinguished by Hierarchical Cluster Analysis and Indicator Species Analysis, representing five previously undescribed tree species associations with unique set of consistent species. Principal Component Analysis revealed two transitional pathways of species dominance along an altitudinal gradient, highly determined by relative topographic position. The level of stand stratification varied within a very wide range, corresponding to physiognomic composition. Rotated-sigmoid and negative exponential diameter distributions were formed by overstorey species with modal, and understorey species with negative exponential distribution. Overstorey dominant species showed extreme nurse log dependence during regeneration, which supports the formation of their modal distribution by an early natural selection process. This allows the coexistence of overstorey and understorey dominant species, increasing the sensitivity of these primary ecosystems to forest management.

Key Words: natural stand reference, nature conservation, nurse log, phytosociology, primary forest

Introduction

Eastern Himalayan temperate conifer forests cover more than 20% of the area of Bhutan, encompassing an outstanding proportion of old-growth stands and some of the highest-altitude forest ecosystems in the world (Olson et al. 2001; Forest Monitoring and Information Division 2023).

These forests provide key habitat for a wide array of endangered and highly vulnerable taxa, including Eastern Himalayan yew (*Taxus wallichiana* Zucc.), coffin juniper (*Juniperus recurva* var. *coxii* A.B.Jacks), red panda (*Ailurus fulgens* F.Cuvier), Bengal tiger (*Panthera tigris tigris* Linnaeus), Himalayan musk deer (*Moschus leucogaster* Hodgson), alpine musk deer (*Moschus chrys-*

ogaster Hodgson), satyr tragopan (*Tragopan satyra* Hodgson) and Himalayan monal (*Lophophorus impejanus* Latham) (International Union for Conservation of Nature 2024).

The rainshadowed inner valleys of Bhutan are characterized by a remarkable variability of topographic, microclimatic and edaphic conditions. Differences in environmental gradients compared to other valley systems in the Eastern Himalayas manifest in unique vegetation zonation and extended altitudinal range of coniferous forests, between 2,200 and 4,200 meters above sea level (Grierson et al. 1983; Ohsawa 1987; McDonald 2016). On the one hand, the lower altitudinal belt is predominantly occupied by semi-xeric, disturbed blue pine (*Pinus wallichiana* A.B.Jacks) stands (Ohsawa 1987; Vilà-Vilardell et al. 2020). Contrastingly, high-altitude sites are covered by virtually undisturbed cloud forests with nearly consistently high relative air humidity in the monsoon season and reduced solar radiation by shallow convective clouds during the dry winter season (McDonald 2016; Forest Monitoring and Information Division 2023). However, the highest compositional heterogeneity can be found in the mid-altitudinal belt, often referred to as the mixed conifer zone, where nearly every tree species of inner valley conifer forests may coexist under the late-successional predominance of Himalayan hemlock (*Tsuga dumosa* D.Don), Eastern Himalayan spruce (*Picea spinulosa* Griff.) and Sikkim fir (*Abies densa* Griff.). In Western Bhutan, this belt is particularly diverse in regard to dominant and codominant tree species, as *P. spinulosa*, *Quercus semecarpifolia* Sm. and *Juniperus* spp. are relatively more abundant in this region (Ohsawa 1987; Rosset 1999; Forest Monitoring and Information Division 2023). Temperate conifer forests in Bhutan have been traditionally divided into five vegetation zones, determined by predominant species (Grierson et al. 1983). Grierson et al. (1983) distinguished Blue pine, Spruce, Hemlock, Fir, and Juniper/Rhododendron temperate coniferous zones. This vegetation classification was consequently converted into conventional forest types (Forest Monitoring and Information Division 2023). While this classification has been utterly useful for ecological studies in Bhutan, there is a lack of research on the variety of tree species communities in the mixed conifer belt.

The coexistence of tree species in old-growth forest ecosystems can be driven by various factors (Wilson et al. 2019). Niche partitioning along environmental gradients may support association between tree species with similar site condition preferences (Whittaker 1956). Furthermore, the spatiotemporal pattern of disturbance intensity can create a spectrum of regeneration niches in regard to light availability in canopy gaps, offering a patch-scale competitive advantage trade-off between species, depending on their shade-tolerance in early life stages (Loehle 2000; Wright et al. 2003; Tenzin 2008). Nonetheless, consistent coexistence of tree species on small spatial scales requires further mechanisms of niche partitioning, such as vertical niche stratification or regeneration microsite differentiation, determined by the life history strategy of species (Takahashi 1997; Kohyama et al. 2003; Easdale et al. 2007). As an example of the latter, nurse log dependent regeneration is a characteristic of particular species in the mixed conifer zone (Darabant 2008). However, our knowledge on whether stratification between coexisting species may contribute to their coexistence in these forests has been limited. Evaluating these factors is fundamental for the conservation of associated species with concerning conservation status. Nonetheless, as different communities may differ in terms of stand structure, providing a reference on community level natural structural characteristics is essential for sustainable management practices in managed forests (Franklin 1993; Larsen et al. 2022).

Therefore, this study primarily aimed (1) to distinguish tree species assemblages within an old-growth, late successional mixed conifer forest in Western Bhutan, and (2) to investigate the compositional and stand structural characteristics of distinguished assemblages, including standing deadwood and coarse woody debris structure. Population structure and regeneration of species were further assessed to evaluate strata niche partitioning and nurse log dependence driven regeneration niche differentiation in the study site, while transitions of species dominance were assessed along influential topographic gradients for the external evaluation of the integrity of distinguished communities (de Cáceres et al. 2015).

Materials and Methods

Study site

The study was conducted in an old-growth Eastern Himalayan mixed conifer forest, located east of Dotenang and Tango monastery in Kawang, Thimphu district, Western Bhutan (27°35'11 N, 89°39'29 E) (Fig. 1). The study site falls under State Reserved Forest status and it is culturally protected, as the area is considered as the home of numerous wrathful deities. The site covers 230 ha between 3,000 and 3,600 masl, vertically restricted by lower altitude disturbed forests with pioneer blue pine (*Pinus wallichiana* A.B.Jacks) and higher altitude Fir zone forests (Ohsawa 1987). The study site is predominantly in northwestern and western aspects, with relatively moderate slopes, mostly between 5 and 30°. The climate is highly monsoon-influenced, with unimodal precipitation regime, very humid, moderate summers, and dry winters (Ménégoz et al. 2013). As the site is located in the northeastern part of Thimhpu Valley, it is relatively more humid. Cloud immersion and convective cloud formation are common, particularly at higher altitudes. The predominant soil types are cambisols, with podzolization above approximately 3,300 masl and sporadic occurrence of stagnosols (Simon et al. 2018), mainly on paragneiss and amphibolite bedrock with occasional out-crops (Long et al. 2011). The overstorey dominant species are Himalayan hemlock (*Tsuga dumosa* D.Don), Eastern Himalayan spruce (*Picea spinulosa* Griff.), and Sikkim fir (*Abies densa* Griff.). These species are frequently mixed with coffin juniper (*Juniperus recurva* var. *coxii* A.B.Jacks), flaky juniper (*Juniperus squamata* D.Don), brown oak (*Quercus semecarpifolia* Sm.), Himalayan holly (*Ilex dipyrena* Wall.), Eastern Himalayan yew (*Taxus wall-ichiana* Zucc.), rhododendrons (*Rhododendron arboreum*
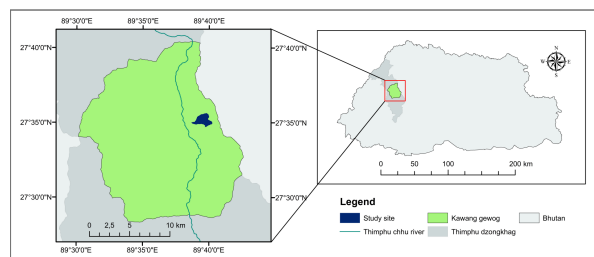
Sm., *R. fulgens* Hook.f., *R. kesangiae* D.G.Long & Rushforth, *R. falconeri* Hook.f., *R. barbatum* Wall., *R. ni-veum* Hook.f. etc.), maples (*Acer campbellii* Hook.f. & Thomson, *A. stachyophyllum* Hiern., *A. cappadocicum* Gled.), Himalayan hazelnut (*Corylus ferox* Wall.) and fra-grant wintergreen (*Gaultheria fragrantissima* Wall.). Smaller areas within the study site had been affected by selective logging in the past. Above 3,300 masl, seasonal forest graz-ing by approximately a hundred yaks has been practiced for a period of up to 2 months annually in the dry season, con-centrated outside the study site.

Data collection

Ninety simple random circular sampling plots were es-tablished in the study site by preliminary generation of cen-ter coordinates. In order to ensure that each sample repre-sents a natural compositional and structural state, sampling plots with signs of past anthropogenic disturbance other than forest grazing were excluded and replaced by a newly generated random plot. Data collection was carried out in spring, 2023. Tree and site data were collected in fixed-area circular plots with 700 m^2 horizontal area (r=14.927 m) (Fig. 2). Horizontal distance measurements with Haglöf Vertex III ultrasonic hypsometer (Haglöf AB) were per-formed to ensure the accuracy of plot borders. The relative position of each stem (DBH ≥ 6 cm) was assessed by meas-uring horizontal distance and compass angle from the plot center to the central axis of the stem. Diameter at breast
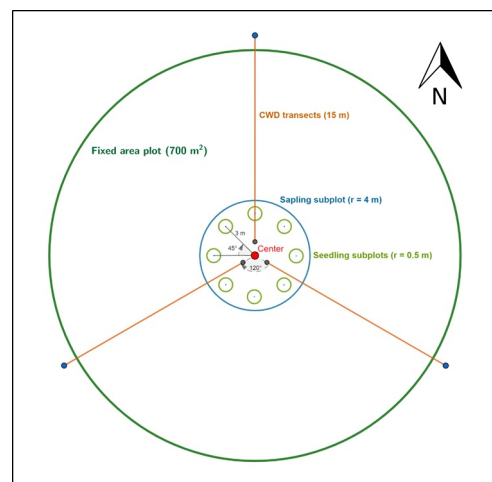

Fig. 1. Geographic location of the study site.

Fig. 2. Sampling plot design.

height (DBH; at 130 cm) was measured and species was recorded. Selective height and four-point crown projection area (CPA) measurements included 60 to 150 individuals per dominant species, depending on the number of diameter classes, representing every class. Height measurements were carried out with Haglöf Vertex III. For standing deadwood (SDW), relative position, diameter, height, and decay class (Sollins 1982) were recorded, along with species when identifiable. Regarding site characteristics, altitude, aspect, slope, cover of specific layers were recorded.

The number of saplings (DBH $\leq$ 6 cm and height $\geq$ 30 cm) was counted by species in two categories (juvenile: 30 cm $\leq$ H $<$ 130 cm; advanced: H $\geq$ 130 cm) within one subplot with 4 m horizontal radius from the plot center. Number of seedlings (H $<$ 30 cm) was counted by species in eight subplots with 0.5 m radius, placed 3 m from the center with 45-degree angular intervals. Shrub and chamaephyte species were assessed in the same manner. Coarse woody debris (CWD) was sampled by the Line Intersect Method (van Wagner 1968) with fan transect layout (Bell et al. 1996). Three 15 m long linear transects were placed at 0, 120, and 240 horizontal degrees starting at 1 m distance from the plot center. In case the transect intersected an angular piece more than once, it was considered a separate observation. The diameter and length of each CWD piece (D$_i$ $\geq$ 6 cm and length $\geq$ 1 m) were measured at the point of intersection of the transect and the centerline of the piece, perpendicularly to the centerline. For pieces with D$_i$ $\geq$ 30 cm, the diameter was additionally measured at the closest point to the two ends of the piece, where the shape was intact. Decay class was recorded in the following categories: 1 - freshly fallen intact logs with or without bark; 2 - mildly decayed with partly soft sapwood and original or near original color; 3 - intermediately decayed with soft sapwood, but hard heartwood; 4 - advancedly decayed with soft heartwood; 5 - very strongly decayed, nearly lost structural integrity (Sollins 1982). The presence or absence of root collar was recorded. However, root collars were not included in length and diameter measurements. The density of seedlings and saplings of tree species were estimated on nurse logs within intervals of 1 per square meter.

Data analysis

To classify sampling plots by tree species composition,

Hierarchical Cluster Analysis (HCA) was conducted with Ward's linkage method and Euclidean distance matrix of both the relative basal area (RBA) and relative stem density of live trees (RD) of each species, as complementary measures of their relative dominance and relative abundance in each plot. HCA was conducted with R software (R Core Team 2021) and package 'amap' (Lucas 2022). The performance of three distance measures (Euclidean, Bray-Curtis and Manhattan) was pre-assessed by Silhouette Width Analysis (SWA, Rousseeuw 1987), conducted with package "cluster" (Maechler et al. 2023). SWA tells us about the compactness and distinctness of clusters to evaluate different clustering algorithms. R package 'dendextend' (Galili 2015) was used for dendrogram visualization. To identify the hierarchical level of tree species assemblages, Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) was carried out based on the mean of RBA and RD of species. ISA reveals the clustering solution with the floristically most unique array of communities based on the mean significance and strength of indication by species concerned (McCune et al. 2002; Pakgohar et al. 2021). The significance of Indicator Values was computed by 10,000 Monte Carlo permutations. ISA was conducted with R package "indicspecies" (de Cáceres and Legendre 2009). In order to identify tree species associations with unique set of consistent co-occurring species (de Cáceres et al. 2015), the compositional profile of assemblages was assessed by the RBA, RD, and the relative frequency of the occurrence of tree species within that particular assemblage. Whitford Index (Whitford 1949) was further calculated to quantify the clumpedness of species occurrence within distinguished assemblages. Larger Whitford index values represent more aggregated distribution of a species within a particular community, with values above 0.05 indicating clumped distribution.

To assess transitional pathways of species dominance and the relationship between dominance gradients and topographic gradients within the study site, principal component analysis (PCA) was carried out with the singular value decomposition (SVD) of the scaled dominance/topographic position matrix. SVD identifies principal components by decomposing the matrix into orthogonal vectors that capture the maximum variance without covariance matrix computation, ensuring numerical accuracy (Lyche 2020). The

scaled variable matrix consisted of the RBA of the seven dominant species and influential topographic variables. In order to detect topographic variables with significant influence on species dominance, Spearman's rho correlation matrix was computed between the RBA of dominant species, altitude, slope, aspect, and Topographic Position Index (TPI, Weiss 2001). TPI is a widely used measure of the relative altitudinal position of a sampling plot compared to the mean altitude of a specific surrounding area. The considered neighbourhood size is dependent on the spatial scale of topographic features in focus. To capture relative topographic position in the context of intermediate-scale topographic features, such as the secondary ridgelines and midslope valleys prominent in the studied forest, TPI with a 750 m radius was an optimal predictor parameter (Weiss 2001). The TPI value of each plot was derived from a 30 m resolution Digital Elevation Model (International Centre for Integrated Mountain Development 2011) in ArcMap (ESRI). Ggplot2 (Wickham 2016), ggfortify (Horikoshi and Tang 2018), and ggrepel (Slowikowski 2011) R packages were used for PCA visualization.

Structural characteristics of distinguished tree species communities were investigated by structural parameters, species-divided diameter distribution of live trees and diameter distribution of standing deadwood (SDW). Conventional parameters included the Basal area of live trees (BA_L), Stem density of live trees (D_L), Basal area of standing deadwood (BA_{SDW}), Stem density of standing deadwood (D_{SDW}), Volume of coarse woody debris (V_{CWD}) and Gini coefficient of diameter differentiation of live trees (GC, Gini 1921; Sterba 2008). GC is a widely used measure of plot-scale structural diversity, based on size differentiation and inequality within each plot (Sterba 2008). The estimated volume of CWD was calculated by van Wagner's formula (1968). Based on these six variables, pairwise PERMANOVA was carried out to assess the significance of overall structural dissimilarity between tree species assemblages. PERMANOVA was performed with R package vegan (Oksanen et al. 2008). Regeneration and shrub layer composition were examined by the stem density of species by height class. Estimated seedling and sapling density of species were compared on ground and coarse woody debris surfaces, by calculating the horizontal surface projection area of each sampled CWD piece.

Results

Classification of tree species assemblages in the study site

Cluster analysis classified sampling plots based on the relative dominance and relative abundance of tree species (Fig. 3). Indicator Species Analyses, conducted on consecutive clustering solutions representing hierarchical levels of HCA revealed that the mean Indicator Value of tree species for their most indicated single cluster was the largest in the case of seven clusters (ISA, $IndVal_{mean}=0.469$ at height= 200). Similarly, the mean p-value of Indicator Values was found to be the lowest for seven clusters ($p_{mean}=0.25$). The second best values were found in the case of eight clusters ($IndVal_{mean}=0.452$ and $p_{mean}=0.276$, at height=175), followed by six clusters ($IndVal_{mean}=0.441$, $p_{mean}=0.292$ at height=300). On the other hand, the hierarchical level of three clusters, corresponding to the conventional forest type classification, resulted in a remarkably higher mean p-value of Indicator Values ($p_{mean}=0.342$ at height=900). The potential better performance of Bray-Curtis and Manhattan distance measures was rejected, as these measures led to higher numbers of misassigned plots on all hierarchical levels, with equal or lower cluster compactness (SWI=0.29, 0.29, and 0.28, for seven clusters with Euclidean, Bray-Curtis and Manhattan distance, respectively). Consequently, the seven tree species assemblages were named by their pre-
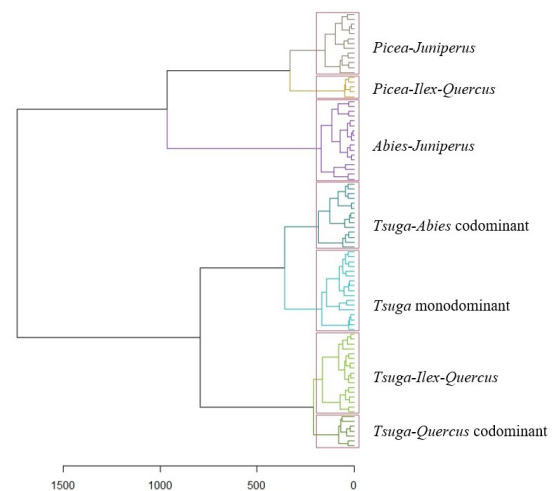

Fig. 3. Dendogram of cluster analysis with the seven distinguished tree species assemblages.

dominant tree species as the following: *Tsuga-Quercus* co-dominant (TQcd), *Tsuga-Ilex-Quercus* (TIQ), *Tsuga* monodominant (Tmd), *Tsuga-Abies* codominant (TAcd), *Abies-Juniperus* (AJ), *Picea-Juniperus* (PJ) and *Picea-Quercus-Ilex* (PQI).

Compositional profile of distinguished tree species assemblages

The compositional profile of distinguished tree species assemblages (Table 1) revealed that *Tsuga-Abies* codominant and *Tsuga* monodominant assemblages are formed by the same set of consistently coexisting tree species. Similarly, *Tsuga-Quercus* codominant and *Tsuga-Ilex-Quercus* assemblages are formed by the same set of consistent species. Both assemblage pairs differ in regard to dominance relations in the upper canopy (indicated by RBA) and specific moderate indicator species. Consequently, five tree species associations were identified (Table 2).

Regarding indicator species, the strongest exclusive singleton assemblage indication was found between *J. recurva* var. *coxii* and *Picea-Juniperus* assemblage (ISA, IndVal= 0.927, p < 0.001). *Tsuga-Quercus* codominant assemblage was characterized by the highest number of indicator species, including *A. stachyophyllum*, *F. paxiana*, and *C. ferox* (IndVal= 0.593, 0.535, and 0.532, respectively, with p < 0.05). However, *A. stachyophyllum* and *C. ferox* were found to be indicative of the combination of *Tsuga-Quercus* codominant and *Tsuga-Ilex-Quercus* assemblages as well, when it was considered as a separate cluster (IndVal= 0.449 and 0.404, respectively, with p < 0.05). *R. fulgens* was a significant indicator for *Tsuga* monodominant assemblage in the study site (IndVal= 0.433, p < 0.05). Other assemblages were characterized by unique sets of non-exclusive indicators.

Certain tree species occurred in several assemblages. According to its Whitford Index values, *P. spinulosa* had

Table 1. Relative basal area (RBA), relative density (RD), and frequency (F) of species and taxon groups in distinguished tree species assemblages

		Tsuga	*Picea*	*Abies*	Q.se.	*Ilex*	J.rec.	J.squ.	T.w.	*Rho.* spp.	*Acer* spp.	Other spp.
PJ	RBA	4.64	**71.76**	7.21	0.53	0.11	10.75	4.05	-	0.76	-	0.19
	RD	6.68	**27.8**	4.02	0.16	0.76	**25.16**	24.47	-	7.92	-	3.04
	F	69.23	100	46.15	7.69	15.38	**92.31**	76.92	-	38.46	-	23.08
PQI	RBA	5.91	**67.14**	0.82	18.5	7.54	-	-	-	0.05	0.03	-
	RD	5.95	**16**	0.41	20.93	55.49	-	-	-	0.82	0.41	-
	F	60	100	20	100	100	-	-	-	20	20	-
AJ	RBA	8.47	12.41	**53.34**	-	-	0.7	22.49	-	2.11	0.15	0.34
	RD	5.09	3.58	**22.71**	-	-	1.51	58.39	-	8.03	0.51	0.17
	F	47.06	58.82	100	-	-	29.41	100	-	29.41	5.88	5.88
TAcd	RBA	**42.74**	12.83	**42.21**	-	0.14	-	0.17	1.64	0.38	0.04	0.04
	RD	**46.84**	9.13	**28.7**	-	0.79	-	1.5	2.13	9.19	0.79	0.93
	F	100	57.14	100	-	7.14	-	7.14	14.29	28.57	7.14	21.43
Tmd	RBA	**80.23**	5.05	10.44	0.09	0.22	0.66	1.25	0.14	1.51	0.2	0.21
	RD	**56.85**	3.01	11.64	0.15	5.12	0.35	0.77	0.88	14.43	1.52	5.27
	F	100	29.41	**76.47**	11.76	23.53	5.88	11.76	11.76	52.94	11.76	23.53
TIQ	RBA	**71.54**	11.17	-	6.40	6.82	-	-	1.56	1.12	0.32	0.21
	RD	18.37	0.95	-	**25.58**	30.54	-	-	2.82	10.67	2.32	1.45
	F	100	52.94	-	94.12	100	-	-	29.41	41.18	41.18	35.29
TQcd	RBA	**49.29**	2.19	-	**40.08**	2.99	-	-	1.49	0.56	1.65	1.75
	RD	**21.13**	2.97	-	13.24	**45.40**	-	-	3.62	3.39	6.49	11.07
	F	100	14.29	-	100	85.71	-	-	28.57	42.86	42.86	**100**

PJ, *Picea-Juniperus*; PQI, *Picea-Quercus-Ilex*; AJ, *Abies-Juniperus*; TAcd, *Tsuga-Abies* codominant; *Tsuga* monodominant; TIQ, *Tsuga-Ilex-Quercus*; TQcd, *Tsuga-Quercus* codominant; Q.se., *Q. semecarpifolia*; J. rec., *J. recurva*; J. squ., *J. squamata*; T.w., *T. wallichiana*; Rho. spp., *Rhododendron* species.

Table 2. Tree species assemblages, along with their corresponding tree species association (based on consistent co-occurant taxa), predominant tree species, outward rounded altitudinal range, and mean Topographic Position Index

Tree species assocation	Tree species assemblage	Overstorey/understorey dominant species	Altitudinal range (masl)	TPI$_{mean}$
Spruce-Juniper (13)	*Picea-Juniperus* (*J. recurva*) (13)	*P. spinulosa* / *J. recurva, J. squamata*	3,350-3,520	0.43
Fir-Juniper (17)	*Abies-Juniperus* (17)	*A. densa* / *J. squamata*	> 3,420	0.07
Hemlock-Fir (31)	*Tsuga-Abies* codominant (14)	*T. dumosa, A. densa* / -	3,230-3,400	-0.12
	Tsuga monodominant (*R. fulgens*) (17)	*T. dumosa* / -	3,120-3,400	-0.41
Hemlock-Oak-Holly	*Tsuga-Ilex-Quercus* (17)	*T. dumosa* / *I. dipyrena, Q. semecarpifolia*	< 3,240	-0.13
(*A. stachy., C. ferox*) (24)	*Tsuga-Quercus* codominant (*F. paxiana*) (7)	*T. dumosa, Q. semecarpifolia* / *I. dipyrena*	< 3,110	-0.28
Spruce-Oak-Holly (5)	*Picea-Quercus-Ilex* (5)	*P. spinulosa* / *I. dipyrena, Q. semecarpifolia*	3,100-3,280	0.42

The number of assigned sampling plots and exclusive indicator species are shown in brackets.
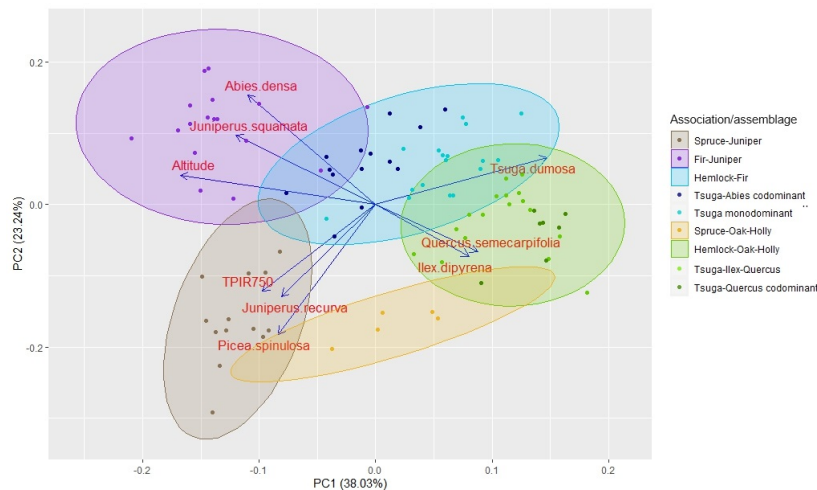

Fig. 4. Biplot of PCA with loading vectors representing the relative dominance of species, altitude, and relative topographic position (TPIR750), along with the 95% probability ellipses of tree species associations and the position of sampling plots colored by tree species assemblage along the first two principal components.

aggregated spatial distribution in *Tsuga-Abies, Abies-Juniperus, Tsuga* monodominant, *Tsuga-Ilex-Quercus* and *Tsuga-Quercus* codominant tree species assemblages (WI=0.22, 0.21, 0.17, 0.17 and 0.15, respectively), corresponding to its occasional local codominance in stands predominated by other species. Somewhat weaker aggregated distribution of *A. densa* was found in *Picea-Juniperus* and *Tsuga* monodominant assemblages (WI=0.16 and 0.14, respectively). *T. dumosa* showed weaker aggregated or clumped distribution in *Abies-Juniperus, Picea-Quercus-Ilex*, and *Picea-Juniperus* assemblages (WI=0.18, 0.1, and 0.07, respectively), corresponding to its a rather transitional

occurrence in the latter two. *R. arboreum* was commonly found in patches throughout the whole study site (17.6% < F < 41.7%). On the other hand, vulnerable *R. niveum* (Gibbs et al. 2011) was found exclusively in the *Picea-Juniperus* assemblage.

Transitional pathways of species dominance

All of the seven dominant species in the study site showed significant correlation with altitude in terms of relative dominance. The RBA of *J. squamata, A. densa, J. recurva* var. *coxii*, and *P. spinulosa* showed positive significant correlation with altitude (Spearman's correlation, r=0.79,

0.67, and 0.45, respectively, with p＜0.001). On the other hand, the RBA of *Q. semecarpifolia*, *I. dipyrena*, and *T. dumosa* negatively correlated with altitude (r=-0.74, -0.71, and -0.63, respectively, with p＜0.001). Regarding relative topographic position, *P. spinulosa* and *J. recurva* var. *coxii* showed significant positive correlation with TPI (r=0.55 and r=0.48, respectively, with p＜0.001), while significant negative correlation was found between *T. dumosa* and TPI (r=-0.49, p＜0.001). Contrarily, none of the dominant species showed significant correlation with slope or aspect regarding their relative dominance. According to their significant influence on species composition in the study site, altitude and TPI were selected for further analysis.

PCA revealed two transitional pathways of species dominance along an altitudinal gradient, partially distinguished by relative topographic position (Fig. 4). The first two principal components explained 61.27% of the total variance and altitude strongly correlated with the first principal component (r=-0.92, p＜0.001). *P. spinulosa* dominated stands

occurred solely in convex relative topographic positions. Relatively continuous transitions were found to be particularly characteristic to *T. dumosa* dominated and codominated tree species assemblages. This manifested in a very high overlap between the probability ellipses of the two intra-association assemblage pairs along the first two principal components, compared to their corresponding tree species associations.

Structural parameters of distinguished tree species assemblages

The mean estimated basal area of live trees per hectare varied within a relatively small range between tree species assemblages (mean±SD=68.7±20.8, N=17 in *Abies-Juniperus* and 83.3±21.2, N=7 in *Tsuga-Ilex-Quercus*). However, it was differently distributed between size classes (Fig. 5). This is reflected in the higher variation of live stem density between assemblages, which was the lowest in *Tsuga* monodominant (mean±SD=222.4±43.3, N=13) and the highest in *Picea-Quercus-Ilex* stands (mean±SD=545.7±179.4, N=5). Pairwise PERMANOVA conducted on the six structural variables (Table 3) revealed that structural characteristics correspond to physiognomic composition, determined by altitudinal zonation. There was no significant structural dissimilarity between mid-altitude *Tsuga-Abies* codominant and *Tsuga* monodominant tree species assemblages (PERMANOVA, $F_{1,29}$=0.954, p=0.345), characterized by very low live stem density in small size classes. Similarly, insignificant structural dissimilarity was found between higher altitude *Abies-Juniperus* and *Picea-Juniperus* assemblages ($F_{1,28}$=0.793, p=0.384), characterized by intermediate stem density of live trees and outstanding stem density of SDW. Furthermore, low altitude *Tsuga-Quercus* codominant, *Tsuga-Ilex-Quercus*, and *Picea-Quercus-Ilex* assemblages, characterized by high live stem density of evergreen broadleaf species, also showed a lack of significant structural inter-assemblage dissimilarity in terms of the six parameters ($F_{1,22}$=0.688, p=0.517; $F_{1,10}$=0.593, p=0.581 and $F_{1,20}$=0.03, p=0.866, respectively).

Diameter distribution of identified tree species associations

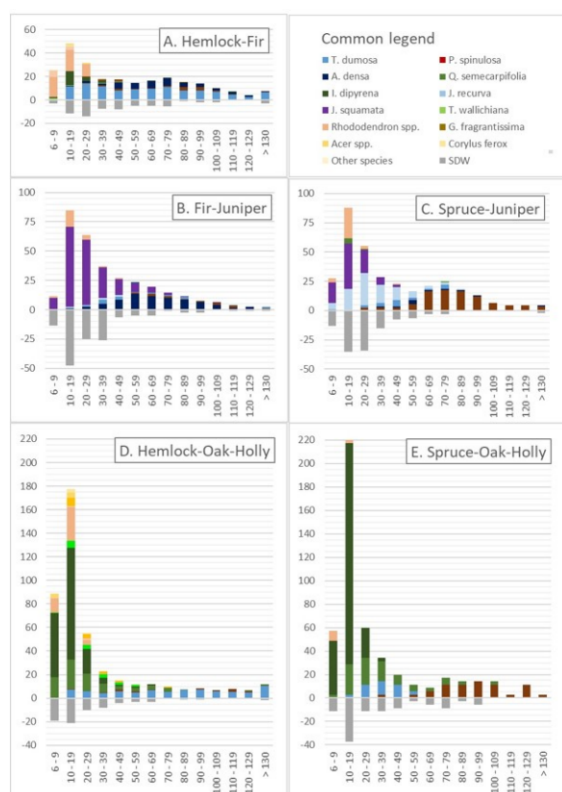Corresponding to the structural and compositional similarity within identified tree species associations, diameter

Fig. 5. Species divided diameter distribution of live trees and diameter distribution of SDW in the five identified tree species associations.

Table 3. Structural parameters in distinguished tree species assemblages and associations

	BA_L (m²/ha)	D_L (N/ha)	GC (0-1)	BA_{SDW} (N/ha)	D_{SDW} (m²/ha)	V_{CWD} (m³/ha)
I. *Picea-Juniperus*	75	350.5	0.39	11.5	129.7	192.9
II. *Picea-Quercus-Ilex*	81.1	545.7	0.44	11.1	71.4	131.7
III. *Abies-Juniperus*	68.7	384	0.37	18.6	152.1	150.5
IV. Hemlock-Fir association	71.4	229	0.35	16.3	67.3	248.2
a. *Tsuga-Abies* codominant	73	222.4	0.31	18	75.5	287.8
b. *Tsuga* monodominant	70	234.5	0.38	14.9	60.5	215.5
V. Hemlock-Oak-Holly association	79.9	467.9	0.48	10.6	76.8	215
a. *Tsuga-Quercus* codominant	78.3	414.3	0.5	11.8	75.5	249.9
b. *Tsuga-Ilex-Quercus*	83.3	489.9	0.5	10.0	77.3	200.6
Study site	74.8	374.2	0.4	14.2	95.1	206.4

BA_L, basal area of live trees; D_L, stem density of live trees; GC, Gini Coefficient of diameter differentiation of live trees; BA_{SDW}, basal area of standing deadwood; D_{SDW}, stem density of standing deadwood; V_{CWD}, volume of coarse woody debris.
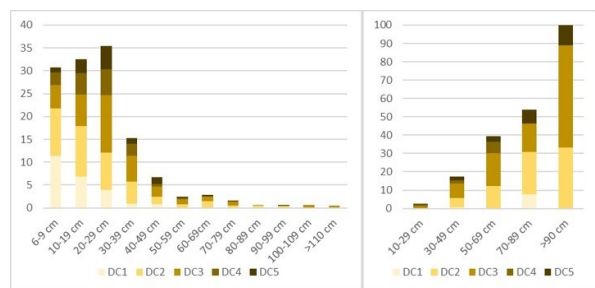

Fig. 6. Decay class divided diameter frequency distribution of CWD per hectare on the study site (left); and decay class divided distribution of the relative density of CWD with seedlings of dominant understorey species in the study site (right). DC, Decay class.

distributions are presented on an association level. The diameter distribution shape of live trees was rotated-sigmoid (RS) in the majority of tree species associations in the study site (Fig. 5). Outstanding RS peaks were found particularly in the Hemlock-Fir, Spruce-Juniper, and Spruce-Oak-Holly associations. However, Fir-Juniper stands were characterized by negative exponential (NE) distribution. These RS and NE shapes are formed by dominant species with unimodal (UM; *Picea spinulosa* and *Abies densa*) or bimodal (BM; *Tsuga dumosa*) distribution, and understorey species with predominantly NE distribution in smaller size classes. Species that occurred in various communities generally maintained parallel distribution shapes throughout. Stands with *Juniperus* spp. dominated understorey showed an outstanding abundance of small size class SDW.

Regeneration and shrub layer composition in distinguished tree species associations

Estimated stem density in the shrub layer varied within a wide range between distinguished tree species assemblages. The stem density of non-chamaephyte shrub species was the highest in *Tsuga-Ilex-Quercus* stands (mean±SE= 6846±734/ha, N=17) and lowest in *Abies-Juniperus* stands (mean±SE=819±240/ha, N=17). *Daphne bholua* (Buch.-Ham.) predominated the shrub layer in every community (RD＞50%). In low- and mid-altitude assemblages, the codominant shrub species was *Berberis precipua* (C.K.Schneid), with (RD＞25%). These assemblages also consisted of extensive bamboo colonies with mean cover of *Arundinaria* spp. and *Yushinia* spp. between 15 and 25%. Several sparsely occurring shrub species (RD＜1%) were found solely in *Tsuga-Ilex-Quercus* and *Tsuga-Quercus* codominant stands, including *Osmanthus suavis* (King ex C.B.Clarke), *Litsea sericea* (Wall ex. Nees), *Lyonia ovalifolia* (Wall.), *Ilex crenata* (Thunb.), *Enkhianthus deflexus* (Griff.). On the other hand, higher altitude *Picea-Juniperus* and *Abies-Juniperus* assemblages were characterized by *Rosa sericea* (Lindl.) codominance in the shrub layer (RD=38.5 and 38.6%, respectively) and lack of excessive bamboo layer. *Gaultheria fragrantissima* (Wall.) and *Pieris formosa* (Wall.) were found sparsely throughout the study site.

Both advanced and juvenile saplings of the four overstorey species were nearly absent on ground surface in the

whole study site ($N_{H \geq 130\ cm}$=1.7/ha; $N_{H < 130\ cm}$= 4.6/ha). Their estimated seedling density on the forest floor was 453/ha. However, the estimated sapling density of these species on coarse woody debris surface was 54.9 times higher, while their estimated seedling density was 18.5 times higher on CWD. The probability of seedling establishment of overstorey species generally increased with increasing size of CWD pieces (Fig. 6). Moreover, saplings of these species on nurse logs were recorded exclusively from pieces with diameter above 30 cm, in intermediate decay classes. Seedlings and saplings of *Juniperus* spp. and *Q. semecarpifolia* were scarcely found on both ground and CWD surface. Endangered *T. wallichiana* and near threatened *J. recurva* var. *coxii* were nearly absent in regeneration.

Discussion

Tree species assemblages and associations in the study site

The occurrence of compositionally distinct tree species communities in the study site was found to be supported by strong pairwise association tendency between overstorey and particular understorey species along altitudinal and relative topographic position gradients. In montane forest ecosystems with seasonal precipitation regime, relative topographic position is commonly among the major drivers of species dominance trade-off (Lan et al. 2011). It influences received solar radiation and evapotranspiration (Mendéz-Toribio et al. 2017), cloud immersion and precipitation (Häger and Dohrenbusch 2011), shallow convective cloud formation (Lu et al. 2023), as well as edaphic conditions, particularly

Table 4. Niche partitioning characteristics and preferred communities of tree species in the study site

Species	Phys.	Role	Niche partitioning	Preferred communities in the study site
Tsuga dumosa	EC	OD	Exposure (↓), altitude (↓)	Hemlock zone
Abies densa	EC	OD	Altitude (↑)	Fir zone
Picea spinulosa	EC	OD	Exposure (↑), altitude (↓), disturbance intensity (↑)	Spruce zone
Quercus semecarpifolia	EB	OUD	Altitude (↓ ↓), disturbance intensity (↑)	Hemlock-Oak-Holly, Spruce-Oak-Holly
Ilex dipyrena	EB	UD	Altitude (↓ ↓)	Hemlock-Oak-Holly, Spruce-Oak-Holly
Juniperus squamata	EC	UD	Altitude (↑ ↑)	Fir-Juniper, Spruce-Juniper
Juniperus recurva	EC	UD	Exposure (↑ ↑), altitude (↑), spruce (↑)	Spruce-Juniper
Taxus wallichiana	EC	STUA	Exposure (↓ ↓), altitude (↓), hemlock (↑)	Hemlock-Oak-Holly, Hemlock-Fir
Rhododendron arboreum	EB	STUA	-	Generalist
Rhododendron fulgens	EB	STUA	Hemlock (↑)	Hemlock-Fir
Rhododendron falconeri	EB	STUA	Hemlock (↑)	Hemlock-Oak-Holly, Hemlock-Fir
Rhododendron kesangiae	EB	STUA	-	Rare (Hemlock communities)
Rhododendron barbatum	EB	STUA	Fir (↑)	Fir-Juniper
Rhododendron niveum	EB	STUA	-	Rare (Spruce-Juniper)
G. fragrantissima	EB	STUA	-	Generalist
Acer stachyophyllum	DB	UA	Disturbance intensity (↑), altitude (↓)	Hemlock-Oak-Holly
Acer campbellii	DB	UA	Disturbance intensity (↑)	Generalist
Acer cappadocicum	DB	UA	Disturbance intensity (↑)	Rare
Corylus ferox	DB	UA	Disturbance intensity (↑), altitude (↓)	Hemlock-Oak-Holly
Fraxinus paxiana	DB	UA	Disturbance intensity (↑), altitude (↓)	Hemlock-Oak-Holly
Betula utilis	DB	PI	Disturbance intensity (↑ ↑)	Generalist
Larix griffithii	DC	PI	Disturbance intensity (↑ ↑)	Generalist

EC, evergreen coniferous; EB, evergreen broadleaf; DC, deciduous coniferous; DB, deciduous broadleaf; OD, overstorey dominant; OUD, overstorey/understorey dominant; UD, understorey dominant; STUA, shade-tolerant understorey associate; UA, shade intolerant understorey associate; PI, pioneer species.

soil humidity and organic matter content (Clark et al. 1999). Nonetheless, it can also influence natural disturbance regime, particularly the intensity of windthrows (de Lima and de Moura 2008). These factors can lead to the competitive advantage of *P. spinulosa* in the regeneration layer along midslope ridgelines within the mixed conifer zone (Tenzin 2008), corresponding to the less shade-tolerant and more mesic character of the species compared to *T. dumosa* (Table 4) (Gratzer et al. 2004). Nevertheless, significant differentiation in shade-tolerance between these species presumably allow the local patch-scale codominance of *P. spinulosa* throughout different communities in the study site, corresponding to a spatio-temporal pattern of disturbance intensity (Loehle 2000).

Picea-Juniperus and *Picea-Quercus-Ilex* tree species assemblages represent two previously undistinguished associations within the Spruce vegetation zone (Grierson et al. 1983). *Picea-Juniperus* assemblage occupied exposed sites between 3,350 and 3,550 masl. Near threatened *Juniperus recurva* var. *coxii* was nearly exclusive and highly indicative of this assemblage in the study site, dominating the understorey, often mixed with *J. squamata* or *R. arboreum*. *J. recurva* is extremely rare in old-growth forests in the Eastern Himalayas (McDonald 2016). However, its occasional occurance in old-growth mixed conifer forests has been observed in Bhutan (Ohsawa 1987). Vulnerable *R. niveum*, a species previously reported only from a few locations (Gibbs et al. 2011; Namgay and Sridith 2020), was found exclusively in this assemblage. On the other hand, *Picea-Quercus-Ilex* stands were found in relatively lower altitude exposed sites. This altitudinal belt around 3,000 masl represents a transitional zone between evergreen broadleaf and cold-temperate coniferous forests in humid and mezic sites in Bhutan, characterized by gradually decreasing relative dominance of *Quercus* spp. and richness of *Lauraceae* spp. in the shrub layer along increasing altitude and decreasing temperature (Ohsawa 1987; McDonald 2016). Considering the geographic and mezoclimatic constrains of the adjacency of *P. spinulosa* and *Q. semecarpifolia* dominated forests (Farjon and Filer 2013; Forest Monitoring and Information Division 2023), *Picea-Quercus-Ilex* tree species assemblage is presumably characteristic to the inner valleys of Western Bhutan.

Contrastingly, lower altitude sites in concave relative topographic positions were found to be inhabited by *Tsuga-Ilex-Quercus* and *Tsuga-Quercus* codominant tree species assemblages in the study site, distinguished by *Q. semecarpifolia* codominance in the upper canopy and the occurrence of *F. paxiana*, a floristic element of evergreen oak forests. Similarly to *P. spinulosa*, *Q. semecarpifolia* codominance in the overstorey can be secondarily supported by relatively larger-scale natural disturbance events in the past, corresponding to the lower shade-tolerance of these species compared to *T. dumosa* (Metz 1997). Characterized by a shared set of consistent co-occurrent species and overlapping niche along topographic gradients, these assemblages represent a unique tree species association with two consequent stages of compositional transition from the Hemlock vegetation zone towards the Evergreen oak vegetation zone (Grierson et al. 1983). However, they compositionally differ from corresponding Hemlock- Evergreen broadleaf transitional communities in outer valleys, where more species of *Quercus* coexist (Wangda and Ohsawa 2006). In accordance with this study, Rai et al. (2018) also found an associate character of endangered *Taxus wallichiana* in *T. dumosa* and *Q. semecarpifolia* dominated forests in Western Bhutan.

On the other hand, *Tsuga-Abies* codominant and *Tsuga* monodominant tree species assemblages represent a relatively continuous transition towards the Fir vegetation zone (Grierson et al. 1983). The coexistence of *T. dumosa* and *A. densa* is characteristic to corresponding altitudes throughout Bhutan, including outer valleys (Wangda and Ohsawa 2006; Forest Monitoring and Information Division 2023). In the study site, the lower altitudinal limit of *A. densa* was found to be nearly proximate to the higher altitudinal limit of *I. dipyrena* dominance in the understorey, while the probability of *A. densa* codominance increased with increasing altitude and TPI. Above 3,200 masl, temperatures are too low for *I. dipyrena* and *Q. semecarpifolia* (Ohsawa 1987), while light conditions in late successional hemlock forests are rather insufficient for *Juniperus* spp., due to the dense canopy structure of *T. dumosa* overstorey (McDonald 2016). Therefore, these communities lack understorey dominant species. However, shade-tolerant *T. wallichiana* was common in the lower canopy, particularly in *Tsuga-Abies* codominant stands. Similarly, the highest richness of *Rhododendron* species was found in *Tsuga* mono-

dominant stands with extensive patches of Eastern Himalayan endemic *R. fulgens* and Bhutanese endemic *R. kesangieae.*

With increasing altitude, *A. densa* gradually gains competitive advantage over both *T. dumosa* and *P. spinulosa* due to its the higher resilience to low temperature (Ohsawa 1987) and heavy snowfall (Rosset 1999). *Abies-Juniperus* assemblage represents a unique tree species association within the Fir vegetation zone, contrastingly to mono-dominant *A. densa* forests with *Rhododendron* understorey (Bürgi 2002). The lower altitudinal threshold of *J. squamata* dominance in the understorey highly corresponded to the lower altitudinal threshold of *A. densa* monodominance in the upper canopy in the study site. Nonetheless, junipers can also reach the upper canopy, as well as DBH above 1 meter. It is important to note that taxonomic classifications of turbinate-shaped seed cone junipers are inconsistent and further genetic studies are needed to evaluate the taxonomic status of *Juniperus* populations, in regard to potentially endemic species in Western Bhutan (Adams et al. 2008; Mao et al. 2010; Adams and Schwarzbach 2012; 2013a; 2013b; Farjon and Filer 2013).

The major limitation of this study is that it was conducted within a relatively small area with constricted ranges of topographic gradients. Therefore, it could not cover a full spectrum of communities and transitional pathways that occur within the mixed conifer zone in the inner valleys of Western Bhutan. Furthermore, the topographic preferences of tree species may shift in sites with different topographic and climatic conditions. Nonetheless, the relative abundance of pioneer species can highly vary between sites in the Eastern Himalayas, corresponding to disturbance regime and edaphic conditions (McDonald 2016). Therefore, further studies are needed to understand how all these factors influence composition in the mixed conifer forests of Western Bhutan.

Structural characteristics of distinguished tree species assemblages

The rotated-sigmoid (RS) and negative exponential (NE) diameter distribution shapes found in the study site are considered the most common distribution shapes in temperate old-growth forests in the absence of large-scale disturbance events (Goodburn and Lorimer 1999; Janowiak

et al. 2008). These distributions correspond to the fine scale of gap formation in late successional mixed conifer forests in the inner valleys of Bhutan (Tenzin 2008), and assume that the studied assemblages are relatively close to a dynamic demographic equilibrium on the studied spatial scales (Alessandrini et al. 2011). Rotated-sigmoid distribution generally indicates U-shaped mortality or growth function (Lorimer et al. 2001; Leak 2002; Piovesan et al. 2005), while NE distribution is associated with constant mortality and growth rates of species along a diameter gradient (Muller-Landau et al. 2006; Westphal et al. 2006). In the study site, however, RS and NE shapes are formed by over-storey species with unimodal or bimodal, and understorey species with NE distributions. The NE distribution of *Abies-Juniperus* stands is likely to be affected by a shift of the unimodal distribution peak of *A. densa* towards the lower diameter classes, presumably due to less optimal site conditions in these higher altitude stands.

The level of stand stratification corresponded to physiognomic composition, predominantly determined by altitudinal zonation in the study site. Lower altitude stands with high abundance of evergreen broadleaf species have an outstanding proportion of their basal area in the understorey, while mid-altitude *Tsuga-Abies* stands often represent one-layered vertical structure. The high density of standing deadwood, particularly dead juniper stems in *Abies-Juniperus* and *Picea-Juniperus* assemblages, indicates a strong selection of *Juniperus* spp. in smaller size classes, amplified by the slow decay of the wood of these species. High basal area of SDW corresponds to the high proportion of stem breakage mortality of dominant species compared to uprooting (Tenzin 2008). Larger basal area of standing deadwood in *Tsuga-Abies* and *Abies-Juniperus* stands may be caused by the lower resilience of *A. densa* against rotting-driven mortality in large size classes (Rosset 1999) or higher sensitivity to epiphyte-induced injuries (McDonald 2016).

Regeneration and modal character of dominant species

Modal distribution of specific tree species within a community is often associated with dynamic processes driven by external factors, including structural or compositional succession after large-scale or synchronized small-scale mor-

tality events, or population decline due to failure of regeneration (Zenner 2005; Diaci et al. 2011). Seasonal forest grazing by yaks reportedly has a minimal negative impact on the regeneration of overstorey conifer species, mainly related to occasional trampling of seedlings (Roder et al. 2002). On the other hand, it can also support tree establishment by decreasing bamboo cover (Darabant et al. 2007). Although the occurrence of synchronized fine-scale gap formation events cannot be ruled out completely, internal factors are explanatory for the modal character of these species in the studied old-growth forest.

The majority of seedlings and saplings of overstorey species were found on relatively large CWD pieces in intermediate decay classes, corresponding to the highly nurse log dependent regeneration of these species (Darabant 2008). Nurse log dependence leads to an amplified early selection process due to spatiotemporal restriction of regeneration within a dynamic microsite mosaic, and limits the density of saplings. Consequently, overstorey species are highly underrepresented in small size classes. Bin et al. (2012) found that the modal distribution of tree species can be caused by a strongly right-skewed U-shaped or L-shaped mortality function, with extreme initial mortality rates compared to relatively low rates in mid size classes, which can be further emphasized by a U- or L- shaped growth function. Therefore, microsite dependence driven early selection process can support vertical niche partitioning when high initial mortality rates are compensated by the low mortality and slower growth of overstorey species in intermediate size classes, corresponding to an ontogenic shift as trees reach the upper canopy (Takahashi 1997; Kohyama et al. 2003; Easdale et al. 2007; Lasky et al. 2015). Furthermore, the diameter distribution shapes of these species in distinguished assemblages in the study site were parallel, regardless of highly different levels of competitive pressure by associated tree and shrub species during regeneration, which emphasizes the importance of a nurse log dependence driven selection process. Similarly, unimodal distributions were found to be characteristic of highly nurse log dependent, late-successional overstorey species *Tsuga diversifolia* and *Picea jezoensis* in sub-alpine old-growth mixed conifer forests in Japan (Nishimura et al. 2005), or *Thuja plicata* in temperate rainforests of the Pacific Northwest (Daniels 2003). A bimodal tendency of *P. jez-*

oensis distribution was found at Mt. Gyebang in South Korea as well (Jang and Park 2010). Extreme nurse log dependence of overstorey species in the study site may be amplified by highly unimodal precipitation regime. As air humidity in the dry season is less limited in the cloud forest belt than precipitation, the importance of moisture absorption by coarse woody debris with mossbed may increase. The relatively more even distribution of *T. dumosa* between size classes in the study site compared to unimodal *P. spinulosa* and *A. densa* corresponds to the lower mortality rates of *T. dumosa* in low light levels and more efficient light growth response of the species under suppression (Gratzer et al. 2004). Nonetheless, *A. densa* can maintain similarly even distributions, as well as a less nurse log dependent character in higher-altitude, monodominant old-growth stands with better light availability in the understorey and higher air humidity (Bürgi 2002).

Endangered *T. wallichiana*, near threatened *J. recurva* var. *coxii*, and *Q. semecarpifolia*, were particularly rare in seedling and sapling stages. Poor regeneration of *Q. semecarpifolia* has been previously reported in Bhutan (Tashi 2004; Covey et al. 2015) and other parts of the Himalayas (Vetaas 2000; Joshi and Anderson 2020). While anthropogenic disturbances, such as litter collection and forest grazing negatively impact the regeneration of this oak species, insufficient quantity of saplings has been reported from barely disturbed stands as well (Sharma et al. 2016). Further studies are needed to investigate the regeneration pattern of *J. recurva* var. *coxii* in mixed conifer forests on larger spatiotemporal scales. Regarding *T. wallichiana*, Lanker et al. (2010) reported significantly better regeneration in natural forests compared to disturbed or managed forests. *T. wallichiana* has been heavily overexploited in other parts of the Himalayas (Pant and Samant 2008; Nimasow et al. 2015), while old-growth mixed conifer forests in Bhutan can provide refuge for this locally protected species.

Conclusion

This study distinguished and described tree species assemblages in an old-growth mixed conifer forest in Western Bhutan, in order to extend our knowledge of the compositional and structural heterogeneity within the mixed conifer zone. Altitude and relative topographic position were found

to be major drivers of species dominance trade-off. Seven tree species assemblages were distinguished in the study site, representing five tree species associations with consistent co-occurrent tree species. These previously undescribed associations exhibit different stand structural characteristics, which suggests that this hierarchical level could be more suitable for forest type classification in high-altitude conifer forests than the currently applied vegetation zone classification based on single predominant species. As the study was conducted within a relatively small area and could not cover the whole spectrum of mixed conifer communities and transitional pathways in the inner valleys of Western Bhutan, further research from sites with different conditions and locations is fundamental to enhance our understanding of the variety of forest communities within the mixed conifer zone in this region. The modal diameter distribution tendency of overstorey species corresponds to an early natural selection process, driven by extremely nurse log dependent regeneration. This dependency supports the coexistence of overstorey and understorey species by creating a sufficient strata niche for the latter. Consequently, forest management can affect the compositional integrity of these ecosystems by removing suitable microsites, inevitably leading to a compositional drift.

Acknowledgements

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