Title

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Topographic and Anthropogenic Factors Shaping Subalpine *Abies spectabilis* Forest in Langtang National Park, Eastern Himalaya

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Abstract

Located in the Himalayas, and situated at the highest altitude worldwide, the subalpine forests have come under human pressure through means of timber logging, livestock farming and tourism, which has brought about the progress of degradation. Thus, it is essential to quantify how forest structure is determined by environmental factors over the range of subalpine zone for better management planning. We investigated the subalpine forest dominated by *Abies spectabilis* in Langtang National Park, Nepal Himalaya, by setting 80 plots of 10-by-10 m scattered over the range of subalpine forest from 3170 to 3810 m a.s.l. on a north-facing slope, and examined the relationship between topographic factors (e.g. altitude and slope inclination), anthropogenic factors (e.g. number of cut stumps and trampling intensity), and forest stand variables (e.g. woody species richness and composition, tree and juvenile density, basal area, and topsoil C/N content). Species richness decreased with altitude, number of fallen logs, and trampling intensity while at the same time, it increased with slope inclination and cut stump density. Stands in higher altitude showed lower tree density and basal area, while higher juvenile density of *A. spectabilis*. Juvenile density decreased with high basal area. Stands on steeper slopes had higher tree density with smaller maximum size on poorer soil. With increasing cut stumps, basal area and soil carbon content decreased while woody species richness and tree density increased, suggesting enhanced stand recovery in response to canopy removal. We conclude that *Abies* population is vulnerable to topsoil removal by trampling and cutting, and that altitude-dependent management is needed.

Key words: detrended correspondence analysis, disturbance, generalized linear model, species richness.

Introduction

Subalpine forests are prone to natural variation in climate (Kullman 1988), and we commonly observe a variety of disturbances and their influence on population structure of tree species in forest ecosystems (North et al. 2004). Population structure of dominant tree species reflects the regeneration/degradation status of the species (Gairola et al. 2014), which represents the forest structure (Zhang et al. 2007). Mountain forests have been described on the basis of altitudinal change. In high altitude, climatic factors such as temperature, precipitation, wind and solar radiation strongly influence the forest structure (Ohsawa 1990; Kira 1991; Krauchi et al. 2000). Besides, all these topography, soil condition and the degree of human disturbances modify the distribution and structure of mountain forests (Krauchi et al. 2000; Gairola et al. 2008, 2009, 2014). Subalpine forests of Nepal Himalaya are distributed at the highest altitude in the world, which provide opportunities to evaluate how disturbances impact the forest structure in such environment.

Subalpine forests in the Himalayas are often dominated by *Abies spectabilis* (D. Don) Mirb. *A. spectabilis* is a tall evergreen conifer occurring in high-altitude Himalayas from Afghanistan to Nepal (Stainton 1972). *Abies spectabilis* usually prefer moist northern slopes (Tabata 2004; Ghimire and Lekhak 2007). On the northern slopes at altitude above 3000 m, it tends to dominate the forest. At moist sites, *A. spectabilis* forest is superseded by *Betula utilis* forest near the forest line. On the southern slopes, in contrast, subalpine zone is often dominated by *Juniperus recurva* forest from 3000 to 3600 m, and by dwarf scrub in alpine zone (Stainton 1972).

Subalpine forests in Himalayas are prone to anthropogenic disturbances due to severe climatic conditions and high-altitude residence of local people (Gairola et al. 2014). There are some studies that examine the role of disturbances on the plant species composition in subalpine forests (Taylor et al. 1996; Kumar and Ram 2005; Gairola et al. 2009; Zhang et al. 2010; Rai et al. 2012). However, the question how topographic and anthropogenic factors jointly affect tree community and stand structure is not yet fully understood in subalpine forests of Himalayas (Qingshan et al. 2007; Gairola et al. 2008; Jiangming et al. 2008; Gairola et al. 2014). Regardless of high-elevation distribution, subalpine forests in the Himalayas have been experiencing strong human pressure through timber logging, livestock farming and tourism, and are facing the progress of degradation, deforestation, and the loss of ecological services for local residents (Stevens 2003; Garbarino et al. 2014).
For the conservation of this unique vegetation and ecological services it provides, it is necessary to evaluate the present status of *A. spectabilis* population and forest-stand conditions over the entire range of subalpine forest in relation to natural and human disturbances. The present study was carried out in the *Abies spectabilis* forest in the Langtang National Park, Nepal Himalaya, so as to address two research questions: (1) by which environmental factors the population structure of *A. spectabilis* is regulated; and (2) how natural and/or anthropogenic disturbances bring about emerging effects on the forest structure at large-scale subalpine landscape. This study aims to contribute to the reduction of forest degradation based on ecological knowledge.

**Study Area**

The present study was carried out in a subalpine forest on north facing slope located around the trekking route passing Cholangpati (with hotels) in the Langtang National Park, Nepal Himalaya (85°15′–86°00′E 28°00′–28°20′N, 3100–3900 m a.s.l.) (Figures 1 and 2). The forest was exclusively dominated by *Abies spectabilis*. At lower elevation as well as higher up to 3500 m on northwestern slopes, evergreen oak forest dominated by *Quercus semecarpifolia* was located (Figure 1). Above the forest limit around 3900 m, shrub of *Rhododendron anthopogon* and *R. lepidotum* replaced *Abies* forest. *Abies spectabilis* in this area grew up to 43 m tall. Subalpine *Abies spectabilis* forest is often fragmented due to human impact in the Langtang National Park, whereas the study area represented subalpine *Abies* forest with high and continuous coverage, with the scatter of meadow patches as deforested gaps (Figure 1). The total area of subalpine forest in the frame of Figure 1 accounts for 2.23 km².

Based on the data of the nearest weather station in Dhunche at 28°7′N 85°17′E, 1982 m a.s.l. (Department of Hydrology and Meteorology, Kathmandu, 2010), mean annual rainfall over 1999-2008 was 2038 mm with the highest monthly rainfall in July at 568 mm, and the monthly mean temperature was highest at 20.2°C in July and lowest in January at 8.8°C (Figure 3). The warmth index (WI) and the coldness index (CI) (Kira 1991) were calculated for three reference altitudes; lower limit (3100 m), mid elevation (3500 m) and upper limit (3900 m) of subalpine *Abies spectabilis* forest in the study site, by assuming –0.6°C lapse rate per 100 m from the Dhunche Station at 1982 m. WI were 51.5, 33.5 and 15.7°C month at 3100, 3500 and 3900 m respectively. Meantime, CI were –5.0, –16.3 and –28.3°C month at 3100, 3500 and 3900 m respectively. These suggest that the forest limit is determined by the growing-season temperature sum at WI =15°C month (Kira 1991; Ohsawa 1990, 1993), and

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**Figure 1.** Vegetation distribution and sampling plot locations in Langtang National Park, eastern Himalaya. Plots of 10-by-10 m in surface area are shown by black circle (location based on GPS records) and the hotels at Cholangpati by filled square in vegetation map. Vegetation map is based on the vegetation classification by Stainton (1972) with the satellite image from Google Map (RgoogleMaps) (http://www.jstatsoft.org/v63/i04/), Esri World Imagery and SRTM 1 Arc-Second Global elevation data using ArcGIS 10.2 for Desktop. Langtang National Park map is based on IUCN and UNEP-WCMC (2016), the World Database on Protected Areas (WDPA) (on-line). [Downloaded Dec. 2016, Version 3.1], available at www.protected planet.net.
the limit of evergreen broad-leaved forest at CI = –10°C month is around at 3500 m a.s.l., corresponding to the midst of the subalpine Abies spectabilis forest in northeast slopes, and to the upper limit of Quercus semecarpifolia forest in northwestern slopes (Figure 1), thus the lack of deciduous broadleaved forest between subalpine fir forest and montane evergreen oak forest can be explained by mild winter in the area.

In the target subalpine forest, there were grazing pressure by yaks (Bos grunniens), cows (Bos taurus), horses (Equus caballus) and sheep (Ovis aries), concentrated during July, August and September. Local people take their cows and sheep in the forest for grazing. The entire ground surface of the study area was covered with mosses, litter and humus layer, whereas sites with high trampling pressure disturbed the ground cover and humus layer, removed with the sign of hoof on the ground surface. We observed the ground surface inside the forest greatly affected by trampling. The ground surface was pressed down some 10 to 20 cm from the original surface level.

The forest has also been influenced by tourism, with Lake Gosainkund (4380 m a.s.l.) being the area attraction center for many tourists. Hoteliers inside the study site (Figures 1 and 2) cut down trees for firewood and timber. Cut stumps of Abies spectabilis and Rhododendron spp. were commonly observed inside forest stands. The hoteliers in the area got permission only to collect dry wood of dead trees from the forest for firewood and timber. Wood of Abies spectabilis is preferred as timber and wood of Rhododendron spp. is as firewood. In some instances, hoteliers removed the bark from the basal region to induce death, and used wood of dead stems. There were some open meadow and/or shrub lands within the subalpine forest zone (Figure 1) presumably due to past human impact.

Methods

In October 2008, we carried out vegetation censuses by setting nine transects along maximum slope angle across altitudinal ranges within the study area. Among these, four transects ended up at the ridge of the mountain slope forming topographic edge of fir forest, while the other five ended up at the forest line. We established 80 plots of 10-by-10 m in slope surface area (Figure 1); the number of plots in each transect ranged from 7 to 12. Using average inclination of slope, we obtained horizontal area of each plot for density calculation. We recorded the geographic location and elevation of each plot using a GPS (Garmin eTrex Vista).

In each of 80 plots, we recorded the number of individual stems of every tree and measured stem diameter at breast height (DBH) 1.37 m above ground level. We categorized individuals into three size categories, namely trees (DBH ≥ 1.0 cm), saplings (DBH < 1.0 cm and top height ≥ 20 cm) and seedlings (height < 20 cm). We define juveniles of Abies spectabilis to be individuals < 1 cm DBH (i.e. seedlings plus saplings). We recorded the presence of shrub species (shorter than 137 cm). Due to the variation in growth forms, some species were recorded in both tree and shrub categories. If the individual plant had no branch below the height of 137 cm, we recorded it a tree; otherwise the individual had profuse branching below 137 cm, we recorded it a shrub.

We divided each plot into four subplots of 5-by-5 m, and recorded the height of all seedlings and saplings of Abies spectabilis occurring only in two diagonal subplots. The degree of trampling intensity was categorized into three classes: category ‘high’ is for plots where more than 50% of ground surface was disturbed due to trampling with pressed surface to 10–20 cm; category ‘middle’ is for plots with 10-50% of surface disturbance by trampling; category ‘low’ is for plots where trampling disturbance was less than 10%. We recorded the geographic location and elevation of each plot using a GPS (Garmin eTrex Vista). Slope inclination and slope aspect were measured by using a clinometer. We counted in every plot the number of cut
stumps (≥ 10 cm cross-section diameter) and fallen logs (≥ 20 cm in basal diameter). From each plot, a soil sample of ca. 200 g wet weight was collected at 15-cm deep from the ground surface. Soil samples were air dried in shade and packed in airtight plastic bags for laboratory analysis. From samples, carbon and nitrogen content was measured in the Ecology laboratory of Central Department of Botany, Tribhuvan University, following Gupta (2000). We made identification of plant species with herbarium specimens. Most of the specimens were identified in the field with the help of floristic references (Stainton and Polunin 1987; Stainton 1988), whereas identification of remaining were made in the Herbarium of Central Department of Botany in Tribhuvan University. Botanical nomenclature followed Press et al. (2000).

The statistical analysis was carried out using R (R core team 2013). For the ordination of species composition, Package Vegan (Oksanen et al. 2013) was used. We examined how stand variables of each plot (tree density of Abies spectabilis, that of other species, juvenile density of A. spectabilis, total basal area and maximum DBH, species richness, soil C content and soil C/N ratio) were related to topographic and anthropogenic factors (altitude, slope inclination, slope aspect, number of fallen logs and cut stumps, and trampling intensity). Categorical variables (slope aspect and trampling intensity) were treated as factorial. For slope aspect, less than 180° were defined northeast (default), and more than 180° to be defined northwest. While analyzing the generalized linear model, altitude was in km and 3.5 km was taken as default mid elevation. In case of slope inclination, 16° (as average) was set default. For trampling, trampling intensity, 'low' was set default. Because saplings were rare compared to seedlings (saplings were present only in 33 plots and few in number), we examined seedlings and saplings of Abies spectabilis collectively, and called juveniles in this study. To examine the variation in composition of woody plant species across 80 plots, we used the detrended correspondence analysis (DCA) (Hill and Gauch 1980) based on the presence/absence records. We used the first axis value of DCA to quantify the community variable to be related to environmental factors. The generalized linear models (Hastie and Tibshirani 1990) was applied to relate forest variables (response variables) and environmental factors (explanatory variables). We used Package MASS (Venables and Ripley 2002) to run negative binomial model for count data. The count-based response variables follow negative binomial (with log-link function), and continuous non-negative variables follow gamma distribution (with log-link function). For DCA, we assumed variation follows Gaussian distribution. The best models are selected by the lowest AIC.

Results

Altogether 25 species were recorded from 80 sampling plots (Table 1). Numbers of species (excluding Abies spectabilis) in each plot were few (Table 2). Detrended correspondence analysis (DCA) (Hill and Gauch 1980) was applied to relate forest variables (response variables) and environmental factors (explanatory variables). We used Package MASS (Venables and Ripley 2002) to run negative binomial model for count data. The count-based response variables follow negative binomial (with log-link function), and continuous non-negative variables follow gamma distribution (with log-link function). For DCA, we assumed variation follows Gaussian distribution. The best models are selected by the lowest AIC.

Table 1. Species and their abundance in 80 census plots

<table>
<thead>
<tr>
<th>Code</th>
<th>Species</th>
<th>Abundance per 80 plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABIES</td>
<td>Abies spectabilis (D. Don) Mirb.</td>
<td>80</td>
</tr>
<tr>
<td>RHOCAM</td>
<td>Rhododendron campanulatum D. Don</td>
<td>64</td>
</tr>
<tr>
<td>VIBR</td>
<td>Vibernum erabecens Wall. ex. D. Don</td>
<td>33</td>
</tr>
<tr>
<td>DAPH</td>
<td>Daphne bholua Buch-Ham. ex. D. Don</td>
<td>23</td>
</tr>
<tr>
<td>BERB</td>
<td>Berberis sp.</td>
<td>21</td>
</tr>
<tr>
<td>SPIREA</td>
<td>Spiraea bella Sims.</td>
<td>14</td>
</tr>
<tr>
<td>BETUTI</td>
<td>Betula utilis D. Don</td>
<td>12</td>
</tr>
<tr>
<td>ARUND</td>
<td>Arandinella sp.</td>
<td>12</td>
</tr>
<tr>
<td>SMIAX</td>
<td>Smilax aspera L.</td>
<td>10</td>
</tr>
<tr>
<td>LON</td>
<td>Lonicera acuminata Wall.</td>
<td>8</td>
</tr>
<tr>
<td>RHOBAR</td>
<td>Rhododendron barbatum Wall. ex. D. Don</td>
<td>7</td>
</tr>
<tr>
<td>LYO</td>
<td>Lyonia ovalifolia (Wall.) Drude</td>
<td>6</td>
</tr>
<tr>
<td>SALIX</td>
<td>Salix sp.</td>
<td>5</td>
</tr>
<tr>
<td>ELAG</td>
<td>Elaegnus parrifolia Wall. ex. Royk.</td>
<td>4</td>
</tr>
<tr>
<td>RHOLEP</td>
<td>Rhododendron lepidotum Wall. ex. D. Don</td>
<td>3</td>
</tr>
<tr>
<td>AGAPE</td>
<td>Agapetes sp.</td>
<td>3</td>
</tr>
<tr>
<td>RHOAR</td>
<td>Rhododendron arboresum Sm.</td>
<td>2</td>
</tr>
<tr>
<td>RHOANT</td>
<td>Rhododendron anthopogon D. Don</td>
<td>2</td>
</tr>
<tr>
<td>ARTI</td>
<td>Artinia sp.</td>
<td>2</td>
</tr>
<tr>
<td>ACER</td>
<td>Acer sp.</td>
<td>2</td>
</tr>
<tr>
<td>SOR</td>
<td>Sorbus microphylla Wenz</td>
<td>2</td>
</tr>
<tr>
<td>HYDR</td>
<td>Hydrangea aspera Buch-Ham ex. D. Don</td>
<td>1</td>
</tr>
<tr>
<td>JASMINUM</td>
<td>Jasminum humile L.</td>
<td>1</td>
</tr>
<tr>
<td>RUBUS</td>
<td>Rubus hypargyrus Edgew.</td>
<td>1</td>
</tr>
<tr>
<td>RIBES</td>
<td>Rubus orientalis Desf.</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 2. Distribution range of forest stand variables across 80 census plots

<table>
<thead>
<tr>
<th>Variables</th>
<th>Minimum</th>
<th>2.5-%</th>
<th>Median</th>
<th>97.5-%</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies spectabilis trees per plot</td>
<td>1</td>
<td>1</td>
<td>6</td>
<td>16</td>
<td>25</td>
</tr>
<tr>
<td>Trees other than Abies per plot</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>14</td>
</tr>
<tr>
<td>A. spectabilis seedlings per plot</td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>82</td>
<td>114</td>
</tr>
<tr>
<td>A. spectabilis juveniles per plot</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>87</td>
<td>155</td>
</tr>
<tr>
<td>Basal area (cm² m⁻²)</td>
<td>3.9</td>
<td>9.5</td>
<td>66.7</td>
<td>161</td>
<td>236</td>
</tr>
<tr>
<td>Maximum DBH (cm)</td>
<td>14.5</td>
<td>18.9</td>
<td>47.0</td>
<td>94.5</td>
<td>167.5</td>
</tr>
<tr>
<td>Soil C per dry mass (%)</td>
<td>2.7</td>
<td>3.8</td>
<td>7.2</td>
<td>9.7</td>
<td>10.5</td>
</tr>
<tr>
<td>Soil C/N ratio</td>
<td>8</td>
<td>11.6</td>
<td>15.5</td>
<td>58.2</td>
<td>107</td>
</tr>
<tr>
<td>Number of woody species per plot</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>11</td>
<td>14</td>
</tr>
<tr>
<td>Altitude (km)</td>
<td>3.17</td>
<td>3.22</td>
<td>3.49</td>
<td>3.80</td>
<td>3.81</td>
</tr>
<tr>
<td>Slope inclination (degree)</td>
<td>14</td>
<td>16</td>
<td>25</td>
<td>36</td>
<td>38</td>
</tr>
<tr>
<td>Number of fallen logs per plot</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Number of cut stumps per plot</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>14</td>
<td>19</td>
</tr>
</tbody>
</table>
based on the presence of species abbreviated the observed variation in woody species composition with 0.16 and 0.08 by the first and second axes. These small contribution ratios of the two axes and the U-shaped dispersion of the second-axis values against the first-axis values are caused by opportunistic and low abundances of minor species. We therefore use the value of DCA first axis only. Species distributions along the first axis suggested no clear separation into groups. *Rhododendron arboreum, R. barbatum, Jasminum humile, Rubus hypargyrus* and *Lyonia ovalifolia* with large values on DCA first axis were found only towards the lower altitude, whereas *Rhododendron anthropogon* with small value on the first axis was found only on higher altitude (Figure 4).

The height distribution of *Abies spectabilis* juveniles (Figure 5A) indicates abundant seedlings far more than saplings. Out of 80 plots *Abies spectabilis* seedlings were present in 72 plots and saplings were present only in 33 plots (Table 2). Frequency distribution of DBH showed inverse-J shape except for the smallest class of DBH < 10 cm (Figure 5B). The range of maximum DBH in each plot were between 14.5 to 167.5 cm (Table 2).

Pairwise correlations among environmental variables show no significant tendency (Table 3A), so that we carried out the examination of how forest variables are explained by the linear combination of environmental variables (as in Table 4). By contrast, forest stand variables were mutually interdependent (Table 3B). The most pronounced relationships were that juvenile density of *Abies spectabilis* and species richness were low in developed stands with high basal area and maximum stem size.

Table 4 shows environment dependence of forest variables. With altitude, tree densities of *Abies spectabilis* and other species, and basal area were decreased while juvenile density of *A. spectabilis* was increased (Table 4). Density of *Abies* juveniles was decreased with trampling intensity (Table 4), and with basal area (Table 3B, Figure 6). Soil carbon-to-nitrogen ratio was lower in higher altitude. Densities of *Abies spectabilis* trees and number of species were higher on steep slopes, while maximum DBH were smaller there (Table 4). The study area has steep slopes ranging from 14° to 38° (Table 2). Increase in slopes brought about the decrease in soil organic carbon content. Soil C/N ratio was generally low across plots (Table 2), meanwhile it was relatively high on steep slopes. Our study area was set on north-facing slope (Figure 1), where we distinguished slope aspect into northeast (NE) and northwest (NW). There was no clear relationship between forest stand variables and slope aspect, while soil C/N ratio were found lower on NW slope than on NE (Table 4).

Anthropogenic factors such as the density of man-cut stumps influenced tree population structure. There were only 26 plots without cut stumps (Table 2). The average cut stump density per plot (surface area of 100 m²) was 2.3. Tree density was higher in plots with more cut stumps while basal area and maximum DBH were smaller in these plots (Table 4). Soil organic carbon content was decreased, and species number was increased with cut stump density (Table 4). Both the number of species and the value of DCA first axis were decreased with altitude, with the number of fallen logs, and with increasing trampling intensity. Meantime, they were increased on steep slopes.

![Figure 4. Results of the detrended correspondence analysis (DCA) based on the presence/absence of woody species in 80 plots. A, ordination of 80 plots; B, species scores on the coordinates of the first two axes. Species are shown by codes in Table 1.](image-url)
Figure 5. A, Frequency distribution in top height of juveniles (< 1 cm DBH); B, frequency distribution in DBH of trees (≥ 1 cm); recorded in all 80 plots. Open, *Abies spectabilis* shaded, other species.

Table 3. Pairwise Pearson correlation coefficients among environmental variables, and among forest stand variables

<table>
<thead>
<tr>
<th></th>
<th>Altitude (km)</th>
<th>Slope inclination (°)</th>
<th>Slope aspect (NW/NE)</th>
<th>Fallen logs</th>
<th>Trampling class</th>
<th>Cut stumps per plot</th>
<th>Non-Abies tree density (m²⁻¹)</th>
<th>Abies juvenile density (m²⁻¹)</th>
<th>Maximum DBH (cm)</th>
<th>Basal area (cm²⁻¹)</th>
<th>Soil C per dry mass (%)</th>
<th>Soil C/N ratio</th>
<th>DCA first axis</th>
<th>Community richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (km)</td>
<td>-0.063</td>
<td>-0.039</td>
<td>-0.101</td>
<td>0.101</td>
<td>0.149</td>
<td></td>
<td>-0.278</td>
<td>-0.039</td>
<td>-0.271</td>
<td>0.052</td>
<td>-0.249</td>
<td>-0.092</td>
<td>0.366</td>
<td>0.246</td>
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<tr>
<td>Slope inclination (°)</td>
<td>0.041</td>
<td>0.055</td>
<td>0.008</td>
<td>-0.041</td>
<td></td>
<td></td>
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<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Slope aspect (NW/NE)</td>
<td>0.085</td>
<td>0.121</td>
<td>0.017</td>
<td></td>
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<tr>
<td>Fallen logs per plot</td>
<td>0.078</td>
<td>-0.104</td>
<td></td>
<td></td>
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<tr>
<td>Trampling class</td>
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</tbody>
</table>

(B) Forest stand variables*

<table>
<thead>
<tr>
<th></th>
<th>Non-Abies tree density (m²⁻¹)</th>
<th>Abies juvenile density (m²⁻¹)</th>
<th>Maximum DBH (cm)</th>
<th>Basal area (cm²⁻¹)</th>
<th>Soil C per dry mass (%)</th>
<th>Soil C/N ratio</th>
<th>DCA first axis</th>
<th>Community richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies tree density (m²⁻¹)</td>
<td>-0.278</td>
<td>-0.039</td>
<td>-0.271</td>
<td>0.052</td>
<td>-0.249</td>
<td>-0.092</td>
<td>0.366</td>
<td>0.246</td>
</tr>
<tr>
<td>Non-Abies tree density (m²⁻¹)</td>
<td>-0.115</td>
<td>-0.039</td>
<td>-0.115</td>
<td>-0.041</td>
<td>-0.258</td>
<td>-0.149</td>
<td>0.361</td>
<td>0.167</td>
</tr>
<tr>
<td>Abies juvenile density (m²⁻¹)</td>
<td>-0.431</td>
<td>-0.539</td>
<td>-0.233</td>
<td>0.014</td>
<td>-0.208</td>
<td>-0.035</td>
<td>0.361</td>
<td>0.167</td>
</tr>
<tr>
<td>Maximum DBH (cm)</td>
<td>0.874</td>
<td>0.244</td>
<td>0.209</td>
<td>0.010</td>
<td>0.191</td>
<td>-0.133</td>
<td>0.361</td>
<td>0.167</td>
</tr>
<tr>
<td>Basal area (cm²⁻¹)</td>
<td>0.209</td>
<td>0.244</td>
<td>0.010</td>
<td>0.191</td>
<td>0.226</td>
<td>-0.133</td>
<td>0.361</td>
<td>0.167</td>
</tr>
<tr>
<td>Soil C per dry mass (%)</td>
<td>-0.176</td>
<td>-0.226</td>
<td>-0.176</td>
<td>-0.226</td>
<td>-0.019</td>
<td>-0.133</td>
<td>0.361</td>
<td>0.167</td>
</tr>
<tr>
<td>Soil C/N ratio</td>
<td>0.052</td>
<td>0.092</td>
<td>0.052</td>
<td>0.092</td>
<td>0.366</td>
<td>0.246</td>
<td>0.053</td>
<td>0.065</td>
</tr>
<tr>
<td>DCA first axis</td>
<td>0.651</td>
<td>0.85</td>
<td>0.651</td>
<td>0.85</td>
<td>0.361</td>
<td>0.053</td>
<td>0.065</td>
<td>0.065</td>
</tr>
</tbody>
</table>

* All forest stand variables except DCA axis are log-transformed.

Bold values are significant (P = 0.05).

Table 4. Dependence of forest stand variables on environmental variables by generalized linear models

<table>
<thead>
<tr>
<th>Objective variables*</th>
<th>Altitude (km)</th>
<th>Slope inclination (°)</th>
<th>Slope aspect (NW/NE)</th>
<th>Number of fallen logs</th>
<th>Number of cut stumps</th>
<th>Trampling intensity</th>
<th>Exp(constant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population variables</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies tree density (m²⁻¹)</td>
<td>-0.90</td>
<td>0.024</td>
<td>0.029</td>
<td>0.029</td>
<td>0.053</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-Abies tree density (m²⁻¹)</td>
<td>1.97</td>
<td>0.098</td>
<td>1.01</td>
<td>1.01</td>
<td>0.0027</td>
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<tr>
<td>Abies juvenile density (m²⁻¹)</td>
<td>-2.3</td>
<td>-0.74</td>
<td>-0.90</td>
<td>-0.90</td>
<td>0.85</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area (cm²⁻¹)</td>
<td>-0.57</td>
<td>0.036</td>
<td>0.036</td>
<td>0.036</td>
<td>79.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum stem diameter (cm)</td>
<td>-3.012</td>
<td>-0.036</td>
<td>-0.036</td>
<td>-0.036</td>
<td>63.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum DBH (cm)</td>
<td>-0.62</td>
<td>0.024</td>
<td>0.029</td>
<td>0.029</td>
<td>0.053</td>
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<td>-0.036</td>
<td>-0.036</td>
<td>63.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil properties</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C per dry mass (%)</td>
<td>-0.51</td>
<td>0.021</td>
<td>0.21</td>
<td>0.21</td>
<td>8.36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C/N ratio</td>
<td>-0.62</td>
<td>0.024</td>
<td>0.029</td>
<td>0.029</td>
<td>0.053</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DCA axis-1 by species abundance</td>
<td>-0.67</td>
<td>0.0074</td>
<td>-0.022</td>
<td>-0.022</td>
<td>0.070</td>
<td>-0.15</td>
<td></td>
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<tr>
<td>Number of species per plot (excl. Abies)</td>
<td>-2.7</td>
<td>0.018</td>
<td>-0.093</td>
<td>-0.093</td>
<td>0.028</td>
<td>-0.074</td>
<td>3.07</td>
</tr>
</tbody>
</table>

* Except DCA axis-1, all objective variables are log transformed; logarithmic horizontal plot area was set to be offset term for count-based density variables; negative binomial distributions were applied for count-based variables and Gamma distribution for other variables except DCA axis-1, where normal distribution was applied.
Discussion
Altitude, topography and disturbance are the important determinants that characterize the structure and composition of subalpine forest (Liu 1997; Grytnes 2003; Gairola et al. 2008, 2009, 2014). The studied forest was poor in woody species diversity (Table 1), and there was no clear differentiation in species composition within the subalpine *Abies spectabilis* forest. Our study suggested tree density, total basal area, and number of woody species were decreased with altitude, which agrees with the previous studies (Yoda 1967; Miyajima and Takahashi 2007; Dang et al. 2013; Gairola et al. 2014). Altitude is linked with climatic environments such as temperature and precipitation (Cierjacks et al. 2008). Low temperature in high-elevation subalpine zone influences tree growth (Zhang et al. 2010), which results in the reduction of density of trees, basal area and maximum tree size. Meantime, Takahashi et al. (2012) suggested the decrease in tree density at high altitude is mainly due to mechanical damage, strong winds and snow deposition, not to low temperature. Subalpine forests are also affected by topographic factors like slope inclination and aspect (Miller and Halpern 1998). The increase in tree density for both *Abies spectabilis* and other species and the decrease in maximum tree size on steep slopes suggest that trees cannot grow large due to unstable substrate stands. On steep slopes, species richness was higher, and species composition tended to be similar to that in lower elevation, which also suggests that there are higher opportunity to find more species in relatively short-statured stands with higher tree density per unit area.

Disturbances are common in subalpine forests (Taylor et al. 1996). High-altitude forests in Himalayas are affected by timber logging and trampling (Kreyling et al. 2008; Gairola et al. 2014; Garbarino et al. 2014). High anthropogenic disturbances via trampling intensity reduce the plant diversity in subalpine forests (Dang et al. 2009; Mingyu et al. 2009; Garbarino et al. 2014). Low- and moderate-class trampling showed less effect on forest-floor moss cover than high-class trampling (Mingyu et al. 2009). The present subalpine forest was highly disturbed by livestock trampling, and where sites with high trampling intensity showed removal of moss and litter cover and humus layer. *Abies spectabilis* juveniles and density of non-*Abies* trees were reduced by increased trampling intensity due to the loss of safe site for establishment, which is consistent with those reported elsewhere (Eilu and Obua 2005; Wehn et al. 2011; Garbarino et al. 2014). Zhang et al. (2010) found decline in seedling density due to trampling by yaks and human interference in southeast Tibet. In the present forest, species composition in plots with high trampling intensity was similar to that in high-altitude plots, and species richness was decreased with trampling intensity.

Our studied forest also experienced logging of trees for timber and firewood. Increasing tourists cause demand for firewood and enhance illegal logging (Garbarino et al. 2014). Tree density of *Abies spectabilis* and species richness were higher in plots with more cut stumps, while basal area and maximum tree size were decreased there (Table 4). The removal of canopy trees may enhance replacement by small-sized trees. Selective removal of dominant and subordinate species, i.e. *Abies spectabilis* and *Rhododendron campanulatum* for timber and firewood respectively, may provide chance for other species to establish. This is a possible reason of higher species richness in plots with higher cut stump density.

Soil properties such as organic carbon and nitrogen content are interrelated with the structural properties of forest stands (Egnell et al. 2015). Topography is an important determinant for soil carbon and nitrogen content in subalpine coniferous forest (Garten 2000). In our study site, soil organic carbon content was found low on steep slopes. Due to direct solar radiation, soil in steeper slopes gets drier (Small and McCarthy 2005), which results in the fast decomposition of soil organic carbon. Meantime, soil C/N ratio was higher on steeper slopes, suggesting higher microbial activities due to increased radiation and soil temperature. Soil C/N ratio declines with increase in elevation (Table 4), which may be due to lower microbial activity in low temperature. Soil carbon and nitrogen content were also varied with disturbances.

In high elevation, forest stands showed sparse canopy layer and dense juvenile layer (Table 4). Even at the same basal area, density of *Abies* juveniles was increased with altitude (Figure 6). In higher elevation, tall trees are damaged by wind and/or snow deposition (Qingshan et al. 2007), and where seedling regeneration is enhanced under better light conditions (Zhang et al. 2010). Similar results have been reported in other

![Figure 6](image_url)
regions (Ghimire and Lekhak 2007; Gaire et al. 2010; Dang et al. 2013; Gairola et al. 2014).

Scattered non-forest gaps observed in the Abies forest zone (Figure 1) are likely caused by intensive pressure of livestock trampling and timber logging. As the present results indicated, Abies population is, to some extent, able to respond to such anthropogenic disturbances with enhanced regeneration. Selective logging indicated by cut stump density can enhance regrowth. It is needed to evaluate the types as well as the threshold intensities of human disturbances for sustainable management of subalpine Abies forests in high altitude Himalayas.

Acknowledgments
We thank Ravi Kumar Sharma and Khumananda Sharma for their assistance in field work, Lea Vegh for making vegetation map, and Junichi Fujinuma and Kosuke Akutsu for data analysis. We also express our gratitude to the Nepalese Department of National Parks and Wild life Conservations (DNPWC) and Langtang National Park, Rasuwa, for giving us permission to undertake this study.

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Subalpine fir forest in east Himalaya


