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Predictors of the Success of Natural Regeneration in a Himalayan Treeline Ecotone

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Abstract: The sensitivity and response of climatic treelines in the Himalayas to climate change is still being debated. Regeneration of tree species in the treeline ecotone is considered a sensitivity indicator and thus of great scientific interest. The aim of this study is to detect predictor variables for regeneration densities of the major tree species in central Himalayan treeline ecotones (*Abies spectabilis*, *Betula utilis*, *Rhododendron campanulatum*), analysing five development stages from seedling to mature tree. We applied negative binomial generalized linear models with predictors selected from a wide range of soil, topography, climate and stand characteristic variables. We found considerably varying predictors across the tree species and their stages of development. Soil conditions, topography and climate, as well as competing and facilitating tree species, had high predictive power for population densities. These predictors were clearly species- and development stage-specific. Predictors' spatial- and development-specific heterogeneity induce a high degree of complexity and diversify any potentially linear response of tree population densities and treeline position to changing climatic conditions.

Keywords: *Abies spectabilis*; *Betula utilis*; competition; life history stages; Nepal; recruitment; regeneration niche; *Rhododendron campanulatum*; saplings; seedlings; species-environment relationships



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1. Introduction

Climatic treelines in high mountains represent elevational limits caused by heat deficiency [1–3]. Consequently, they are often considered to be sensitive bioindicators of global warming cf. [4], supported by the response of treelines to climatic oscillations throughout the Holocene [5–7]. Treelines will shift to higher elevations as a response to climate warming, at least in the long term. Non-thermal site factors, including biotic interactions such as competition, might prevent a short- or mid-term change in treeline elevation. Empirical studies in mountain ranges across the globe found advancing treelines, but in many cases also a distinct persistence of treeline elevations [8,9], suggesting that process dynamics in many treeline ecotones are, to some extent, decoupled from climate warming. Many-faceted interactions between climate warming as an input variable at a global/regional scale, and the complexes of abiotic and biotic site factors, as well as anthropogenic influences and their interrelationships at the landscape/local level, might cause inconsistent response patterns [4].

Most Himalayan treelines are anthropogenic treelines, lowered from their natural elevational position by long-lasting human impacts. Upslope shifts of these treelines are

mostly driven by declining land use intensity, while the changing climate plays a minor role. However, climate change drives dynamics of near-natural treelines, still existing in some remote locations cf. [10]. These treelines thus far show rather low responsiveness to climate warming since the process of climate tracking is being retarded by diverse lag factors and feedback processes in which the krummholz zone plays a crucial role [10–12]. Nevertheless, increasing stand densification, as well as intense tree recruitment within Himalayan treeline ecotones, indicate the potential for future treeline shifts [4,10–18]. Recent dendrochronological studies at Himalayan treelines show climate change-induced constraints of tree growth, with moisture supply in the pre-monsoon season potentially becoming an effective control of future treeline dynamics cf. [4,19].

Abies spectabilis (Himalayan Silver Fir, conifer), *Betula utilis* (Himalayan Birch, deciduous) and *Rhododendron campanulatum* (Bell Rhododendron, evergreen) are dominant tree and krummholz species in upper subalpine forests and treeline ecotones of east-central and east Nepal [20,21]. In light of the still-debated sensitivity and response of climatic treelines in the Himalayas to climate change, these species and their regeneration under changing climate conditions are considered indicators of the future treeline shift potential, and are thus of great scientific interest cf. [4,11].

Observed high levels of recruitment of treeline tree species, as well as environmental niche modelling, suggest that near-natural Himalayan treelines will advance to higher elevation under climate warming conditions, at least in the medium to long term (order of decades to centuries) [11,22]. However, the establishment of seedlings and a successful performance during early life stages is the prior condition for any treeline advance to higher elevations [10]. Combined effects of varied environmental variables usually predict natural regeneration performance [1,17,23,24]. Species-specific competitive strength of seedlings and the interrelationships of local-scale environmental conditions, microsite characteristics and regeneration patterns at treeline ecotones will result in spatially varying treeline dynamics [11,12]. For instance, microhabitat characteristics determine species-specific safe sites for successful seedling establishment. *Abies spectabilis* germinates and establishes preferably on litter accumulations, while seedlings of *Betula utilis* and *Rhododendron campanulatum* occur mainly on bryophyte mats [16]. While substrate differs, all three species depend on shelter elements like rocks or deadwood ameliorating germination and growth conditions. Comparing juvenile individuals and adult trees, Schwab et al. [25] showed that sites with high density of *Abies* and *Betula* individuals of both development stages differ from sites dominated by *Rhododendron*: in contrast to *Rhododendron*, *Abies* and *Betula* occur in high density at warmer and more nutrient rich sites. These sites show more homogeneous surface structures containing large boulders at some sites, while small rock fragments do not have a considerable structuring effect. As well, within plot variation in terms of aspect, slope and curvature is low. This pattern is more pronounced in the case of adult trees compared to juveniles. Temperature seems to play a more important role for *Betula* recruits in comparison to *Abies* recruits, while this relation is inverted in the case of adult trees of the same species [25]. Other environmental variables influencing recruitment success in Himalayan treeline ecotones include competition [26] and light conditions [18,27]. Mainali et al. [17] predict mortality and density of three *Abies spectabilis* and *Rhododendron campanulatum* size classes by variables representing elevation, physical environment and competition, highlighting canopy cover and distance from treelines as significant predictors with size class- and species-specific effects. Development stage-specific, as well as facilitation effects, on seedling performance are analysed by Kambo and Danby [28] at subarctic alpine treelines. At Himalayan treelines, however, detailed studies on varying influences of abiotic and biotic controls over the entire life history from youngest seedlings to adult trees have not yet been conducted. In particular, a multitude of potential explanatory variables, thoroughly characterising environment, competition and facilitation, has not yet been included in regeneration studies at Himalayan treelines.

The identification of variables influencing regeneration and growth performance of tree recruits and explaining the variation in development stage-specific tree species densities

across treeline ecotones might reduce the aforementioned research deficits and provide new insights into regeneration and competition patterns and the sensitivity to climate change. In this paper, we analyse the gradually varying competitive situation, as well as changes of environmental conditions during the life history from youngest seedling to mature tree. We aim at detecting predictor variables for population densities of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum*, differentiating between five development stages from seedling to mature tree. We selected predictors for the 15 respective models from a wide range of available soil, topography, climate and stand structural variables. We hypothesize that variables show major species-specific and development stage-specific differences in explaining variation of tree population densities, and that the significance of climatic variables varies across species and life history.

2. Materials and Methods

2.1. Study Site

We studied the treeline ecotone of the north-facing slope of east-central Nepal's Rolwaling valley (Figure 1, 27°52' N; 86°25' E). Vegetation along the investigated elevational gradient from c. 3700–4200 m a.s.l. has remained in near-natural state due to remote location, low human population density and the Buddhist motif of a sacred hidden valley [29]. Influence of fire, woodcutting, herbivores and domestic animals has been negligible cf. [12,30]. Accordingly, the Rolwaling treeline represents a climatic treeline. The lower part of the ecotone comprises the uppermost subalpine closed forest extending up to c. 3900 m a.s.l. with tall and upright growing *Abies spectabilis*, *Betula utilis* and *Acer caudatum*. Above the treeline, a nearly impenetrable *Rhododendron campanulatum* krummholz zone is developed, followed upslope by alpine dwarf shrub heaths in the upper part of the ecotone above c. 4000 m a.s.l. cf. [12,31,32]. Müller et al. [33] classified soils in the Rolwaling treeline ecotone as podzols. Dry and cold winters and monsoonal, hyper-humid cool summers characterize the study area's temperate climate conditions [34–37].

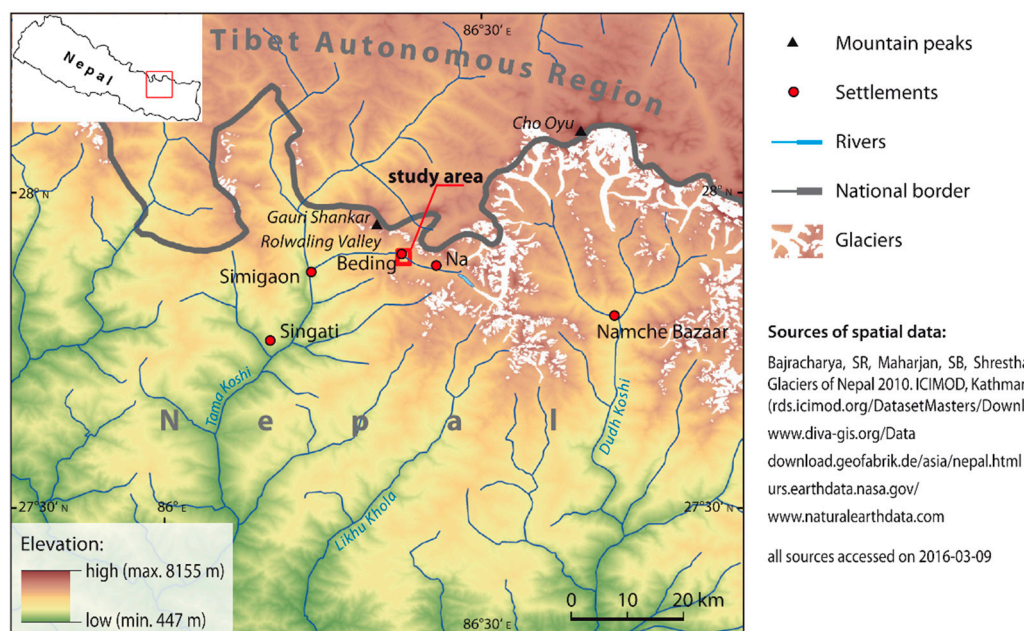


Figure 1. Location of the study area in east-central Nepal.

2.2. Data Collection, Processing and Analyses

We selected in total 34 plots of 20 m × 20 m along the elevational gradient by a stratified-random sampling scheme. Tree species were determined based on Press et al. [38] and Watson et al. [39]. We identified, counted and measured individuals of tree species.

We assigned individuals to height and diameter at breast height (dbh) classes (cf. Table 1). To prepare response variables for generalized linear models, we assigned all individuals from the three target species *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* to one of five development stage classes based on height and dbh (Table 1). We calculated densities of individuals per hectare for each class, resulting in 15 response variables.

Table 1. Parameters and description of development stage classes.

Development Stage	Height [cm]	Diameter 130 cm above Ground [cm]	Description
1	0–10	<7	smallest seedlings
2	>10–50	<7	large seedlings
3	>50–130	<7	small saplings
4	>130	<7	large saplings
5	>130	≥7	mature/adult trees

We calculated densities (individuals per hectare) of juvenile (dbh < 7 cm) and adult (dbh ≥ 7 cm) individuals of each of the six occurring tree species to be used as explanatory variables. These are, in addition to the target species, *Acer caudatum*, *Prunus rufa*, and *Sorbus microphylla*. In addition, we estimated the cover of all vegetation layers. Leaf area index and related light intensity parameters were determined by hemispheric photography [40,41], Appendix 5 of [25]. Moreover, we used seasonal as well as annual soil temperature, soil moisture and air temperature, the latter derived from temperature lapse rates of the study slope [35,37,42]. Soil chemical and physical data of each plot was provided by the Laboratory for Soil Science and Geocology at the University of Tübingen (see [42] for details). We collected topographic data and information on surface structure, e.g., cover with large stones, fine soil etc. cf. [30]. Please see Table S1 (Supplement) for a comprehensive list of all 71 captured potential explanatory variables.

We composed initial model-specific explanatory datasets intuitively according to our expert knowledge (cf. Table S1, Supplement). Then, we checked all potential predictors of variable sets for collinearity using a threshold of $|r| > 0.7$ [43]. We excluded variables resulting in non-collinear predictor sets (cf. Table S1, Supplement). Excluded variables might act as predictors in the final models in a similar way as the selected variables. These might substitute excluded ones to some extent. Thus, we considered excluded variables partially in the results and discussion sections to characterise modelled species environments. Given the high number of up to 39 remaining, uncorrelated variables, we further reduced these potential predictors specifically for each of the 15 response variables by the Boruta feature selection method with 100,000 runs applying random forest with 50,000 trees as an importance source [44–47]. We dropped variables, which were rejected by at least 75% of 50 Boruta selection iterations and used only the remaining ones for building the generalized linear models (cf. Table S1, Supplement).

We tested several models and chose negative binomial generalized linear models with log-link according to the response variable data distribution and results of thorough checks by diagnostic plots and statistics [48–54]. We included only predictors that were constitutively selected by Boruta. On the one hand, inclusion of interactions between potential predictors might improve the obtained models; on the other, interaction terms would considerably increase the number of potential models and make interpretation difficult [55]. Thus, we did not include interaction terms. We selected the final predictor sets by applying best subset regression with Akaike's Information Criterion for small sample sizes (AICc) as selection criterion [28,53,56]. We calculated conditional effects of final model predictors which were conditioned on mean values of all other predictors of the model [57]. Moreover, we estimated average partial effects, a measure for the predictors' average effect on the response, which is backtransformed on linear scale and conditioned on the influence of the other predictors of the model [52,58,59]. To ease interpretation of these final predictor coefficients we standardized predictor values. We prepared and

analysed data and produced figures using the statistical software environment R [60] with functions of, among other packages, Boruta [46], car [52], corrplot [61], DHARMA [54], effects [52,62,63],ggeffects [57], ggstatsplot [64], ggtext [65], margins [59], MASS [66], mfx [67], MuMIn [56], psych [68], ragg [69], various tidyverse-Packages [70] and vcd [71].

3. Results

We sampled in total 8010 individuals of the three target species, of which 3486 belonged to seedlings (development stages 1 + 2), 3262 to saplings (development stages 3 + 4) and 1262 to adult trees. We found *Abies spectabilis* individuals at 65%, *Betula utilis* at 68% and *Rhododendron campanulatum* at 94% of the 34 sampled plots. This ratio was similar across development stage subsamples. Seedlings occurred as follows: *Abies* development stage 1 individuals were present at 35% of the plots while 47% of the plots contained development stage 2. These percentages were 15% and 50% for *Betula* and 79% and 74% for *Rhododendron* (cf. Figure 2 for counts and details of saplings and adult trees). Any plot without one or more of these species were located above treeline, apart from one plot void of *Abies* below. *Abies* and *Betula* occurred at 15% of plots above treeline each, and *Rhododendron campanulatum* occurred at 41%.

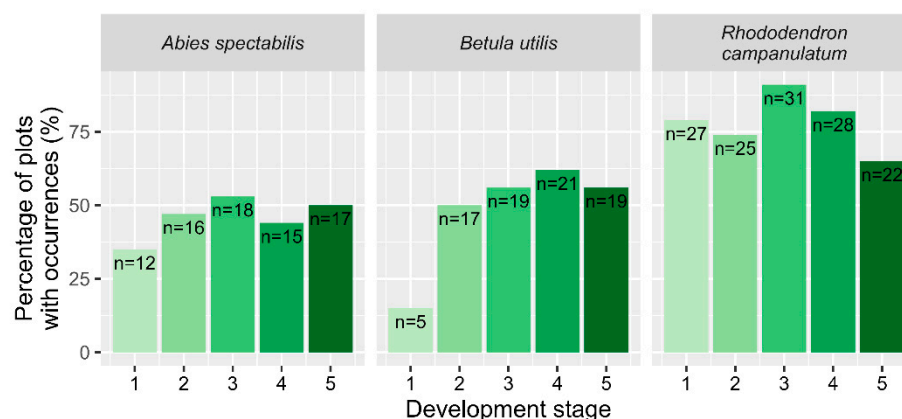


Figure 2. Percentage of plots with occurrence of the target species' development stages (1: smallest seedlings, 5: adult trees). Numbers on bars show basic plot counts (total number of plots: $n = 34$).

The species- and development stage-specific predictor variables of all three investigated tree species showed a complex pattern of mostly three to four (min.: 1, max.: 5) predictors per development stage. A comparison of the predictors of the three species revealed that predictors of the same development stages rarely correspond to each other (Figure S1, Supplement). Moreover, almost all predictors of all three analysed species are superseded by other ones over the life history from stage 1 to 5 (Figure 3). In many cases, one variable contributed to two or three successive stages. Average effects of predictors differed distinctly in magnitude and direction, indicating strongly varying influence on the response. For instance, soil manganese content negatively influenced the density of *Rhododendron* throughout development stages 1 to 3. However, the effect on stage 2 was on average c. 1.5 times stronger and on stage 1 even c. 4 times stronger compared to the effect on stage 3 (please refer to Figure 3 and Figure S2, Supplement and discussion for details).

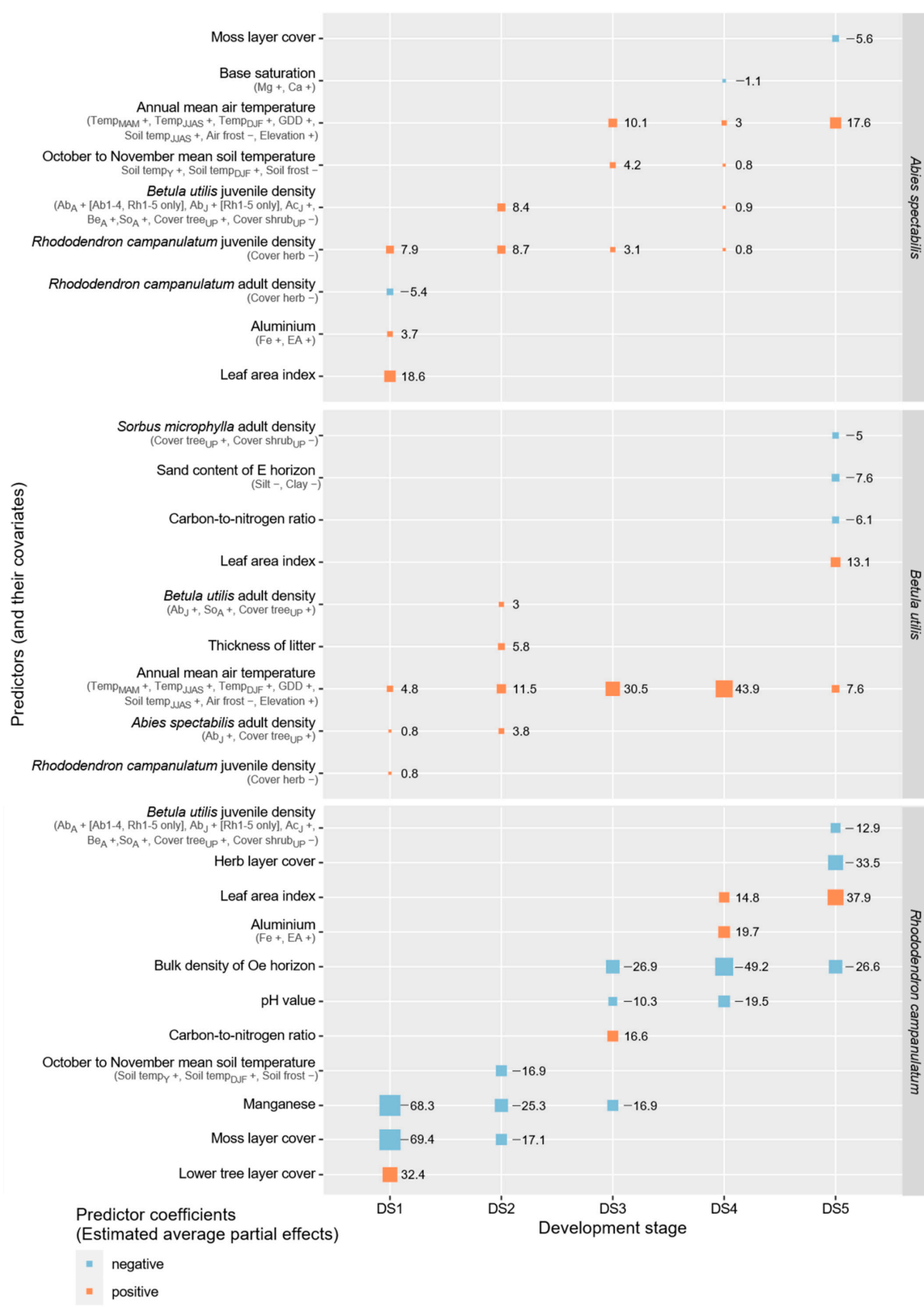


Figure 3. Predictors of the 15 development stage- and species-specific models and their estimated partial effects. Order of predictors highlights their shifting through development stages. Square size corresponds to the magnitude of partial effects. It indicates the predictors' contribution on the

response scale, conditional on the other variables involved. Values are on a response scale (“back transformed” from negative binomial to linear scale), standardized and are thus comparable. Please see Figure S1 (Supplement) for an arrangement of predictors and species, highlighting that the predictors are species-specific, Figure S2 (Supplement) for an impression of changing influences of predictors along their gradients, and Figure S3 (Supplement) for confidence intervals, and to Table S1 (Supplement) for decoding of variable abbreviations.

According to glm predictors, various temperature-related variables influence the densities of *Abies spectabilis* and *Betula utilis* development stages positively, while low soil temperatures facilitate the density of development stage 2 of *Rhododendron campanulatum*. No temperature variable was important for any other *Rhododendron* development stage. Soil and air temperature-related variables were found to positively influence *Abies* individuals of development stages 3 to 5. Likewise, models of all stages of *Betula* included those predictors (cf. Figure 3).

Soil chemical and physical variables acted mainly as predictors for densities of *Rhododendron campanulatum* development stages: Low manganese contents caused high *Rhododendron* densities in development stages 1 to 3. Likewise, pH showed a negative effect on the development stages 3 and 4 densities of *Rhododendron*. Development stage 3 related positively to the carbon-to-nitrogen ratio and stage 4 to aluminium content. Bulk density of Oe horizon predicted *Rhododendron*’s development stages 3 to 5 with a negative relation, i.e., low bulk density is associated with high numbers of *Rhododendron* individuals. Soil parameters rarely predicted *Abies spectabilis* and *Betula utilis* densities: Aluminium (and/or correlating iron) influenced development stage 1 of *Abies* positively, while base saturation (and/or correlating manganese and calcium contents) affected stage 4 negatively. The carbon-to-nitrogen ratio and a coarse soil texture (percentage of sand content) had negative effects on the development stage 5 density of *Betula*. Litter thickness was a positively related predictor for development stage 2 of *Betula*.

Various variables, which characterized vegetation layers’ cover and occurrence of competing tree species, contributed significantly to predictions of tree densities of all species and nearly all development stages. Juvenile *Rhododendron* individuals and/or the correlated cover of the herb layer had positive effects on development stage 1 density of *Betula* and all *Abies* development stages except stage 5. Densities of development stages 2 and 4 of *Abies* were predicted by *Betula* recruit density with positive effect. Various variables correlated to this predictor, i.e., juvenile *Abies* and *Acer* individuals, adult *Abies*, *Betula* and *Sorbus* trees, and cover of shrub and tree layers could potentially perform in a similar way. In addition, *Betula* recruit density contributed significantly and with negative effect to the *Rhododendron* development stage 5 model. The density of adult *Abies* trees was included in the *Betula* development stage 1 and 2 models, while density of *Betula* adult trees was important for the *Betula* development stage 2 model only (all positive effects). Both last-mentioned predictors correlated to other potential predictors, and amongst others, juvenile *Abies* individuals’ density. The leaf area index variable was significant for models of development stages 4 and 5 of *Rhododendron*, stages 1 of *Abies* and 5 of *Betula* (all positive effects). Please see Figure 3 for further predictors and their effects.

4. Discussion

We revealed species- and development stage-specific predictor variables for all 15 GLMs. The significance of single predictors varied throughout the life history from youngest seedling to mature tree. However, temperature-related predictors influenced all *Betula* development stages positively. The GLM predictors roughly resembled important environmental variables of an earlier ordination-based study on the same treeline ecotone cf. [25]. Results of the present study defined species-environment relations more precisely due to additional variables characterising competition, facilitation and light conditions, due to the

more precise attribution of predictors to species and, most importantly, due to much finer subdivided development stages in the present study.

4.1. *Abies spectabilis*

In contrast to larger individuals, temperature did not contribute significantly to predictions of *Abies* seedling densities (development stages 1 + 2); predictors characterising soil conditions and especially neighbourhood had much higher predictive power in this respect. Dense populations of all species (except *Abies* itself), as well as the resulting high leaf area index, were found to positively impact *Abies* seedling density. Although temperature is often regarded as significant for germination success and seedling survival, herb, shrub and mature tree cover can influence microclimate requirements of seedlings to a similar extent; e.g., by mitigating desiccating insolation and wind exposure [28,72]. On the other hand, competition might limit seedling establishment more than temperature [73]. In line with our results, Bürzle et al. [16] highlighted shady conditions and short dispersal distance associated with *Abies spectabilis* seedlings. Seedling and sapling numbers of other *Abies* species (e.g., *Abies alba*) and other shade-tolerant species are known to be positively related to abundance of the same species [74], while admixture of birch further ameliorated regeneration conditions [75]. Several studies point to the positive effect of moist conditions at shady *Abies* germination and seedling sites [72,76]. Cool and moist conditions usually characterize the habitat of *Abies spectabilis* [21], corroborated in this study as the microsite characteristics of *Abies* seedlings, and are marked by such conditions, created by the dense forest canopy. The negative effect of adult *Rhododendron* density on the smallest *Abies* seedlings' density might point to potential loss of these seedlings rather by leaf burial than by insufficient light conditions, as observed for the impact of *Rhododendron* litter on conifer seedlings [77,78]. Other negative *Rhododendron* litter effects include allelopathic effects [10,16]. Negatively collinear to adult *Rhododendron* density, herb cover was found to negatively impact the smallest *Abies* seedlings, in line with findings on the impact of herbaceous cover on the survival of other treeline species' seedlings [79].

The significant, positive effect of temperature on sapling density (development stages 3 + 4) suggest that later, more robust development stages are less affected by desiccation. These larger *Abies* development stages were absent from the upper parts of the investigated transect with harsher climatic conditions, occupied by the wind and sunlight exposed dwarf shrub heath. We assume that low temperatures at these sites affect *Abies* saplings negatively since their growth and occurrence depend on sufficient temperature [15,19,80]. We suggest that temperature also acts as proxy for elevation and consequently for the harsh environment, reducing *Abies* sapling density cf. [81] for *Abies* saplings at Rocky Mountain treelines and contributing to positive temperature effects in our models. Surface characteristics and microtopography did not predict *Abies* seedling and sapling densities, quite similar to findings of a study on spruce and fir recruitment in high elevation forests of British Columbia [82]. The strong positive effect of temperature on predicted densities of *Abies spectabilis* saplings and mature trees (development stage 5) corresponds to predominant occurrences of taller and adult *Abies* individuals at lower elevated parts of the treeline ecotone [25], in line with the common elevational species distribution pattern [21]. In summary, the *Abies spectabilis* models support our hypothesis of variables changing their predictive effects across development stages.

4.2. *Betula utilis*

Temperature had a positive impact on *Betula utilis* density, similar to larger saplings and adult *Abies* individuals, and in line with previous results [25]. In contrast to *Abies*, all development stages of *Betula* showed this effect. Apart from the temperature effect, seedlings of *Betula* were predicted with positive effects by a neighbourhood potentially consisting of juvenile and adult *Abies spectabilis*, adult *Betula utilis* and *Sorbus microphylla*, and juvenile *Rhododendron campanulatum*. Some of these variables showed positive collinearity to each other and also to the upper tree layer cover. This rather shady environment is to

some extent in contradiction to results of other studies stressing the dependence of *Betula* germination on canopy openings [27,83] and light intensity [16,84,85]. However, predictors most likely showed competitive relations rather than the degree of canopy closure as the leaf area index did not contribute to the *Betula* seedling and sapling models. Moreover, even shady conditions obviously provide sufficient light for the species [21]. In addition, the result points to a protective effect of the canopy for seedlings against high irradiation, temperature and associated dry soil conditions at this high-elevated treeline ecotone. Accordingly, Shrestha et al. [27] stressed the dependence of *Betula utilis* seedlings not only on light but also on sufficient soil moisture. This effect might play a role especially for small-seeded tree species such as *Betula* and shallow rooted seedlings [86–88]. With increasing tree size, predictors shifted to positive effects of finer, more favourable soil texture in terms of water retention capacity (reduced percentage of sand fraction), as well as to positive effects of soil fertility (indicated by narrower carbon-to-nitrogen ratio), and to a negative effect of adult *Sorbus microphylla* density. Obviously, these broadleaved species compete with each other for light, similar to other co-occurring *Betula* and *Sorbus* species [89,90]. As reported in other *Betula utilis* studies, tree density and basal area positively correlate to soil nitrogen and to organic matter, while tree growth positively correlates to moisture availability [27,91,92]. Obviously, *Betula utilis* lives up to the expectations of a pioneer species: Our models of seedling and sapling density suggest that apart from sufficient temperature and moisture, no strong effects of other site conditions are needed for successful establishment and growth.

4.3. *Rhododendron campanulatum*

Percentage of moss cover was found to negatively influence seedlings of *Rhododendron campanulatum* in our study. At first glance, this result seems to contradict the findings of Bürzle et al. [16] who detected bryophyte mats as safe sites for *Rhododendron* seedling establishment. While the latter study investigated the microsite characteristics in closest vicinity to seedlings, the present study captured population density and habitat characteristics at a much larger spatial scale. We used ground cover variables indicating general plot rather than specific microsite characteristics. The negative relationship of *Rhododendron* seedling density with the percentage of moss cover points to less moist microhabitats at *Rhododendron* dominated sites as in the krummholz zone compared to subalpine mixed forest. Nevertheless, the soil surface of these sites, mainly covered by slowly decomposing *Rhododendron* litter, could contain moss patches as seedling habitats. Further, our model predicted a positive effect of adult tree cover on *Rhododendron* seedling density, pointing to a certain shade-tolerance of this species. This supports the results of Sharma et al. [18], who recorded a higher seedling density below than above treeline. In the same study, seedling mortality decreased significantly at sites without tree cover above treeline. Similarly, all our models of *Rhododendron* development stages beyond the youngest seedlings lacked positive tree cover effects.

Soil manganese content was an important predictor with negative effect for *Rhododendron* seedling and small sapling densities. Manganese deficiency causes inhibition of growth of most species and lowers competitive strength of tree species. However, competitive strength of low nutrient users such as *Rhododendron* species increases under nutrient deficient conditions [10,12,25], also suggested by the positive effect of carbon-to-nitrogen ratio (less nitrogen availability) in the model of small *Rhododendron* saplings. In addition, high soil acidity at *Rhododendron* dominated sites, caused by the slowly decomposing litter of the species itself, leads to increased plant availability of even small manganese contents [93]. When reaching the development stages of saplings, pH and soil aluminium content became important predictors, showing that acid soil conditions give competitive advantage to the ericaceous *Rhododendron* species [25]. Soil bulk density predicted sapling and tree density with considerably strong negative effect. The considerably negative effect of bulk density of the Oe horizon (dominated by moderately decomposed organic material) in the models for *Rhododendron* sapling and tree densities reflects the poor decomposability

of *Rhododendron* litter. *Rhododendron* is comparatively well adapted to the thick, poorly stabilising ground conditions of such a horizon. According to our observations, *Rhododendron campanulatum* grows vital and up to tree size even with partly laying stem position, supported by shallow and wide-reaching roots. The effects of leaf area index (positive) and percentage of herb layer cover (negative) are associated with the dense, light detaining canopy at *Rhododendron* dominated sites (especially in the krummholz zone). The negative predictive effect of juvenile *Betula* density and the collinear low densities of all other occurring tree species illustrate the extraordinary competitive strength of adult *Rhododendron campanulatum* trees at suitable sites. This negative relation of density of adult *Rhododendron* to other species' densities was already apparent in the ordination of Schwab et al. [25]. Obviously, competition rather than facilitation shapes interactions of adult *Rhododendron* individuals with other species in tree, shrub, and herb layers. The competitive situation will probably aggravate in case of a climate warming-induced stand densification cf. [26]. In comparison to Schwab et al. [25], results of the present study more clearly show that *Rhododendron campanulatum* density is independent of temperature rather than negatively influenced. Instead, soil and competition variables have important effects, similar to our findings for *Abies* seedlings. In contrast to our study, aspect and slope contributed significantly to explain *Rhododendron campanulatum* and *Abies spectabilis* densities of various size classes in a study by Mainali et al. [17]. However, sampling design, model type and initial explanatory variable sets of this study differed considerably.

4.4. Cross-Species Considerations

Apart from few exceptions, we found positive effects of neighbouring vegetation in the 15 models comprising all investigated species and development stages. Obviously, facilitative effects, buffering harsh environmental conditions, often outweigh competition, corroborating results of other studies in treeline environments [94,95]. However, negative biotic interactions have been detected as well, especially in the case of early development stages [78,96]. Examples of this study include the negative effect of adult *Rhododendron* density on *Abies* seedlings and the negative relation of adult *Rhododendron* density to *Betula* recruit density and herb cover, even though this is significant only in the *Rhododendron* development stage 5 model. Our models explain density rather than absence. Thus, they could not sufficiently capture the previously shown strong effect of *Rhododendron* density on *Abies* and *Betula* being nearly absent in the dense *Rhododendron campanulatum* krummholz zone cf. [10,12,25,96].

We did not find a clear pattern of changing predictors along the sequence from germination, seedling and sapling stages to adult trees as described, for instance, by Kambo and Danby [28]. In our case study, factors created by the neighbourhood, mainly light and competition associated with species-specific competitive strengths and requirements add complexity to and modify a common pattern, especially in the case of *Abies* and *Betula*. In addition, variation of the predictors along the rather short gradients of the investigated treeline ecotone might be too low to capture substantial turnovers in predictive effects. Finally, analysing only spatial patterns of seedlings, saplings and mature trees might reveal facilitative and competitive effects more precisely cf. [26] compared to a more comprehensive study, including 71 potential explanatory variables.

In summary, our results are additional confirmation of the fact that climatic treelines are caused by heat deficiency [1–3]. At the same time, the results confirm the complex influence of abiotic and biotic local site conditions in treeline ecotones, their interactions and feedback systems including competition [1,4,10,94], qualifying the role of alpine treelines as bioindicators of climate change. These complex effects of site conditions and their interrelationships control current species-specific recruitment performance, as well as consequential spatial patterns, and are subjected to ongoing modifications by future climate warming inputs.

5. Conclusions

The results indicate that climate is but one of several major variables controlling population densities and treeline dynamics in treeline ecotones under climate change conditions. Various abiotic and biotic variables were identified to control treeline ecotone tree species density with changing significance during life history from youngest seedling to mature tree. The results support an increased focus on varying habitat requirements of adults and juveniles, having received too little recognition in studies of treeline responses to climatic variability to date. Successful recruitment is an essential prerequisite for any treeline shift. Therefore, more detailed investigations of species-specific seedling establishment and recruitment intensity are needed in order to further accentuate the suitability of treelines as bioindicators of climate change. We conclude that there is a distinct need for future studies that acquire and analyse comprehensive explanatory data sets to detect variations throughout life history of competitive and facilitative patterns, as well as of abiotic and biotic species-environment relationships. Regarding central Himalayan treelines, development- and species-specific insights will enhance the understanding of potential changes of the competitive strength of the *Rhododendron campanulatum* in the krummholz zone of treeline ecotones under climate change conditions and will improve the predictive ability regarding the upslope migration of treeline tree species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13030454/s1>, Table S1: Variables used for model building and their features; Figure S1: Predictors of the 15 development stage- and species-specific models and their estimated partial effects. Arrangement of species and predictors highlights that the predictors are species-specific; Figure S2: Conditional effects of each of the predictors of the 15 models; Figure S3: Average standardized partial effects of predictor coefficients on response scale conditioned on other predictors.

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