

## Downhill shift of alpine plant assemblages under contemporary climate and land-use changes

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**Abstract.** Compositional changes in Himalayan vegetation in response to the major drivers of biodiversity loss, climate change and land-use change, are barely documented. We quantify temporal changes in the alpine vegetation of central Nepal and attribute these changes to temporally varying climatic and land-use factors. We re-surveyed the alpine vegetation of two locations within Langtang National Park, central Nepal, after 25 yr using 127 plots of 100 m<sup>2</sup>. Using ordination, regression, and weighted average regression and calibration techniques, we analyzed the changes in terms of species abundance, frequency, and elevational shift in relation to changing atmospheric temperature, precipitation, and livestock grazing. We found a significant increase in the frequency and relative abundance of the majority of species, which was significantly related to the temporal trends in climatic factors and grazing intensity. Out of 12 species with unimodal responses along the elevation gradient during both surveys, the optima of eight species decreased over the time period. The observed elevations of 62 out of 92 sample plots (hence, species composition) in 2014 were lower than the elevations calibrated from species composition and elevation of 1990, indicating an overall downward shift of species assemblages. However, an upward shift of assemblages was also observed at higher elevations. These results indicate that the observed temporal changes in alpine vegetation, largely contrasting the expected upslope shift of species due to climate warming, are driven most likely by interactions of contemporary climate and land-use changes, especially reduced grazing. The complex interactions and feedback mechanisms between warmer winters, increased precipitation, reduced grazing pressure, and thereby altered species interactions most likely facilitated the downslope shift of alpine species assemblages. Climatic and land-use responses of plant species assemblages should therefore be studied focusing on the potential interactions between both the climatic and the land-use factors because such interactions and feedback mechanisms have potential to mask or modify the expected climatic or land-use response of biodiversity.

**Key words:** alpine vegetation; climate change; grazing; Himalaya; land-use change; ordination analysis; species composition; temporal changes.

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### INTRODUCTION

Changes in plant species composition due to climate and land-use changes have been documented for several vegetation types throughout the world (Parmesan and Yohe 2003, MEA 2005, Newbold et al. 2015). However, challenges and uncertainties

still remain despite numerous attempts to analyze the responses of species assemblages to climate and land-use changes at different spatial and temporal scales. Climate change exhibits a heterogeneous spatial pattern, and its nature, intensity, and frequency may be completely redistributed from one spatial scale to the next (Garcia et al. 2014).

Similarly, the type, intensity, and frequency of land-use change differ significantly among geographic regions and vegetation types (MEA 2005, Newbold et al. 2015), and sensitivity to environmental change also varies among species and vegetation types (Parmesan 2006). Because of this variation, the patterns of climate-driven changes revealed at one spatial scale or for one vegetation type may not necessarily reflect those at other scales or for other vegetation types. Moreover, the climatic responses of species are often masked and modified due to confounding factors, such as land-use changes (see Lenoir et al. 2010, Bhatta and Vetaas 2016). A paucity of standard vegetation and land-use data from many biodiversity-rich regions, such as the Himalayas, makes the task even more challenging. Therefore, it is worth analyzing the effects of temporally varying climate and land-use regimes on Himalayan plant species assemblages that represent different vegetation types and that are in different geographic locations.

The climate in the Himalayan region is changing at a faster rate than the global average, which may pose a serious threat to the unique biodiversity of the region (Shrestha et al. 2012). Additionally, there are rapid changes in land-use regimes in the region, such as changes in the livestock grazing patterns, harvesting of plant resources, landscape management, and land abandonment (Singh et al. 2011, Paudel et al. 2016). Significant changes in the treeline position and in the phenology of species in response to the changing climate and land-use regimes have been documented in the region (e.g., Shrestha et al. 2012, Hart et al. 2014, Schickhoff et al. 2016). In particular, increasing trends in winter temperatures (WT) and monsoon (June–August) precipitation have been recorded in the alpine region of central Nepal over recent decades, as has been observed for the whole high Himalayan region (IPCC 2013). Although most alpine plants are dormant during the winter season, there are several crucial ecological processes that may be indirectly influenced by a higher WT, such as the length of the growing season, thereby regulating the alpine vegetation dynamics (Kreyling 2010, Williams et al. 2015). Abrupt change in the WT accompanied by increased summer precipitation is therefore expected to have serious consequences for alpine vegetation dynamics and ecosystem functioning. Changes in plant species assemblages in response

to climate warming and land-use changes may alter the species interactions, thereby leading to modifications in the geographical distributions of species and their assemblages (Lenoir et al. 2010). Despite the changes, the climatic and land-use responses of Himalayan biodiversity have not yet been documented systematically, largely due to a lack of historical records of vegetation and climate in the region. Most of the climate change-related studies from the region are focused on glacial dynamics and hydrology (e.g., Shrestha and Aryal 2011, IPCC 2013 and references therein), treeline dynamics (e.g., Schickhoff et al. 2016 and references therein, Suwal et al. 2016), and the phenological response of species (e.g., Shrestha et al. 2012, Hart et al. 2014). However, climate-driven changes in species composition and geographical distribution are not well documented (but see Telwala et al. 2013, Bhatta and Vetaas 2016, Dolezal et al. 2016).

Alpine vegetation of the Nepal Himalaya (roughly 4100–5000 m a.s.l.) is unique and critical for several reasons. In this zone, there is dramatic variation in the environment and vegetation over small spatial distances, with rich plant diversity and high endemism (Vetaas and Grytnes 2002). The zone represents the upper distributional limit of the majority of vascular plant species. Above this zone, species distributions are limited by extreme low temperature, a scarcity of soil water, limited space, and other harsh conditions such as frost and snow. However, the distribution of higher alpine species toward lower elevations is also limited by the canopy cover of treeline species and a dense layer of bushes just above the treeline. These species are likely stressed by the harsh alpine environment and the direct effect of climate change, and they also must compete with species from lower elevations that are extending their ranges upward to track their climatic niches under ongoing climate change. This has been evidenced by changes in species composition in several alpine areas of the world (e.g., Walthers et al. 2005, Odland et al. 2010). Therefore, the cold-adapted alpine species have neither enough suitable space (to shift further their distributions) nor the sufficiently long time (as the competition imposed by newly shifted species from lower elevations and the direct impacts of climate and land-use changes on the alpine vegetation might be ever rising and acting concurrently) to respond

to climate warming. Consequently, high Himalayan vegetation may be under severe threat of compositional changes and species extinctions. It is therefore urgent to develop a more complete and real-time understanding of how ongoing regional climate changes, together with potential land-use changes, are driving temporal changes in high Himalayan plant assemblages.

We aim to quantify the temporal changes in the alpine vegetation of central Nepal and relate the observed changes to climatic factors that have changed over time. We also attempt to explain how the observed changes qualitatively relate to other potential factors in the region, such as land-use change (mainly grazing), because we currently lack quantitative information about ongoing land-use changes in the region. We posed the following research question: Are there systematic changes in alpine species assemblages of central Nepal that have been driven by climate change and land-use change from 1990 to 2014?

If the changes are documented, we investigate the plausible causal links by testing following hypotheses:

*Hypothesis 1:* If warming climate is the major driver of compositional changes, we would expect an increase in abundance of majority of the species toward higher elevations.

*Hypothesis 2:* If the land-use change (reduced grazing) is a major factor of compositional change, we would expect an increase in species abundance, especially in areas with high density of domestic herbivores in the past.

The hypotheses are not mutually exclusive because temperature and land-use may interact and cause unexpected patterns of species compositions.

## MATERIALS AND METHODS

### Study area

In 2014 (July–October), we re-surveyed the vegetation of two locations within the Langtang National Park, central Nepal: the Yala mountain (Site 1; 28°12' N and 85°35' E) between 4000 and 5000 m a.s.l., and the Pangsang mountain (Site 2; 28°10' N and 85°23' E) between 3850 and 4400 m a.s.l. (Fig. 1). The sites were previously sampled from March to December 1986 (Miehe 1990), hereafter termed “1990 survey.” The Pangsang–Yala mountain range is part of the central Himalayan

region and falls within the subalpine/cool to alpine/cold climate zones (Miehe et al. 2015). Approximately 650 mm of precipitation falls annually, and snowfall is frequent throughout the winter months (Bhatta et al. 2015). Average monthly temperatures recorded from the nearest weather station (Kyanjing weather station, 3920 m a.s.l., ~5–10 km from the sampling locations) range from  $-6.13^{\circ}$  to  $3.63^{\circ}$ C (winter) to  $6.44$ – $11.43^{\circ}$ C (summer; unpublished data from the Department of Meteorology and Hydrology, Nepal, from year 1988 to 2010).

Vegetation of the area consists of subalpine/upper montane and alpine associations (Miehe et al. 2015). The forest limit in the area is at ~3800 m a.s.l. The subalpine vegetation (~3000–4000 m a.s.l.) is characterized by the predominance of *Abies spectabilis*, *Betula utilis*, and *Rhododendron campanulatum*. However, on the drier slopes, *Juniperus recurva* is associated with the shrubby rhododendrons. Alpine vegetation between ~4000 and 4300 m a.s.l. consists of dwarf shrubs such as *Ephedra gerardiana*, *Rhododendron lepidotum*, and *Rhododendron setosum* and herbs in the genera *Anemone*, *Pedicularis*, and *Primula*. The upper alpine zone between ~4300 and 5000 m consists of alpine meadows dominated by cushion-forming species and graminoids.

### Data sampling

*Historical data extraction.*—We extracted the vegetation data of 108 relevés (96 in Site 1 and 12 in Site 2, with 246 vascular plant species between 3850 and 5120 m a.s.l.) for which there were vegetation and elevation records in Miehe (1990). The vegetation in the 1990 survey was sampled by the classical Braun-Blanquet approach, where each species in a relevé was recorded on a cover-abundance scale of + to 5. We avoided the relevés along glacial debris, cliffs, waterbodies, and fire-impacted areas.

*Vegetation re-sampling.*—We used information in Miehe (1990) to find the previously surveyed areas and to locate the geographic position and elevations (based on provided contour maps) of the relevés and their species composition. We sampled 129 plots (80 in Site 1 and 49 in Site 2) of  $10 \times 10$  m along eight transects in these areas. Vascular plant species were recorded on a modified Braun-Blanquet's cover-abundance scale of 0–7 (sensu van der Maarel 1979), and the

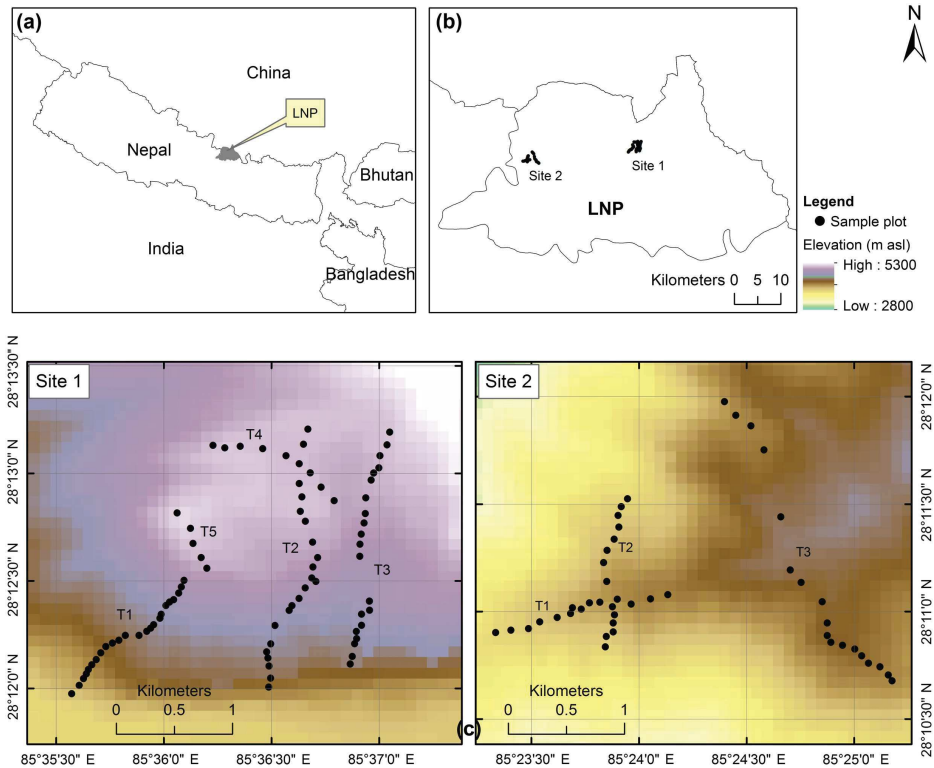


Fig. 1. Map of the study area. (a) Location of Nepal with the study area, Langtang National Park (LNP), shaded; (b) location of the sampling sites; and (c) location of the sample plots in each site.

elevation (m a.s.l.) of each sample plot was measured using a Global Positioning System (Garmin eTrex10). Altogether, 269 species were recorded from both sites.

*Data preparation.*—Although we followed the sampling methodology of the 1990 survey as precisely as possible, a preliminary analysis of the vegetation data revealed several differences between the two surveys regarding the sampling technique, the sample relocations, and the nature of the sampled data.

Typical preferential vegetation sampling technique was applied for the 1990 survey (see Miehe 1990), whereas the 2014 survey applied a non-preferential sampling scheme. Data generated from different vegetation sampling techniques have

their own merits and demerits depending on the scale and purpose of the study (Diekmann et al. 2007, Bhatta et al. 2012a). However, the data generated both by preferential and by non-preferential sampling technique can be used for testing ecological hypotheses if treated with caution, if appropriate statistical tools are applied, and if the results are ecologically interpretable (Diekmann et al. 2007, Lepš and Šmilauer 2007, Økland 2007, Roleček et al. 2007). Accordingly, the historical datasets of phytosociological sampling units have been widely used for assessments of recent vegetation changes (e.g., Tingley and Beissinger 2009, Kapfer et al. 2016 and references therein).

There was a high taxonomic mismatch between the datasets, and it was not sure whether it was

just due to misidentification of the species or was census bias in either or both of the surveys. There were also differences regarding the total number of sampling units, number of sampling units in each 100-m elevation band, range of elevation gradient covered, cover-abundance scale of the sampled species, etc.

Therefore, we performed data pruning applying a very conservative criteria for selection of sampling units and the species for analyses while minimizing potential sampling bias, taxonomic inaccuracies, and census biases. The historical dataset had more samples from higher elevations, whereas the 2014 dataset contained more plots from lower elevations. Therefore, we partitioned the elevation gradient into 50-m elevation bands and matched the elevation and vegetation type of the sample plots vs. relevés in each band. Furthermore, to avoid potential taxonomic and census bias, we only selected the species that were shared between both studies and had more than 3% frequency in either dataset. We had 92 final sample plots of 2014 and 93 relevés of 1990 with 61 species in common. To avoid the estimation bias of cover and abundance, we converted the cover-abundance scores to presence (1)–absence (0) for the overall ordination analysis. For the gradient analysis, we further separated the dataset into two sites, and species with a single occurrence and plots/relevés with less than three species were removed. Thus, we had 56 species (62 plots/68 relevés) in Site 1 and 28 species (12 plots/12 relevés) in Site 2. However, we used standardized abundance data for the weighted average (WA) analyses because we could not assign species' weights with the presence–absence data.

#### *Estimation of explanatory factors*

*Climatic gradient in time and space.*—There is a strong spatial climatic gradient along elevation, where both temperature and precipitation decrease linearly with increasing elevation. Additionally, there is also a significant increasing temporal trend in mean winter minimum temperature (WMT) and annual precipitation (AP), as revealed by the 23-yr (1988–2010) data from the nearest weather station (Appendix S1: Figs. S1 and S2). We estimated the temporal climatic gradient by calculating the 5-yr mean of both the climatic factors for each survey (1988–1992 for the 1990 and 2006–2010 for the

2014). The mean WMT values of 1990 and 2014 were then used to estimate the atmospheric temperatures of the 1990 and 2014 plots, respectively, using the lapse rate (0.51°C per 100 m elevation) for Nepal (Dobremez 1976). Similarly, we also estimated the AP for the 1990 and 2014 plots using the elevational precipitation trend for alpine regions in Nepal (sensu Acharya et al. 2011). Because we used spatial gradient (elevation) to estimate the temporal climate gradient for the sample plots, the temporal and spatial climate gradients may be confounded to some extent.

*Grazing gradient in time and space.*—Inhabitants of Langtang valley (2800–3900 m a.s.l.) and surrounding areas practice transhumance for their livelihoods. Livestock grazing has been especially intense in the areas below ~4500 m a.s.l., and it gradually declines toward the higher alpine belt. This is because the productivity of the pastures remains highest between 3500 and 4000 m a.s.l. and it declines toward higher elevations due to low cover of the high-alpine species, and also because livestock reach rarely above this elevation (Bauer 1990). Consequently, there is a spatial gradient in grazing, which decreases with increasing elevation. However, there have been significant reductions in the populations of typical alpine grazers such as yaks, sheep, and goats over the past decades (Bhatta et al. 2012b, GoN-CBS 2013, Aryal et al. 2014), resulting in a significant reduction in grazing intensity mainly in lower alpine regions (3800–4500 m a.s.l.), as observed elsewhere in the high Himalayas (Banjade et al. 2008, Aryal et al. 2015). Such changes in the grazing regime over time result in a temporal grazing gradient, where more substantial reductions in grazing intensity have been experienced at lower elevations than in high-alpine areas. Historical quantitative data on grazing are lacking for the area. However, selective grazing of livestock in pastures creates a spectrum of species based on their palatability, competitive capacity, and life-form characteristics (Miehe et al. 2009). Therefore, we interpreted the effect of grazing regime changes using temporal trends in grazing indicator species.

Using information from field inspections, local herders, and the literature (Bauer 1990, Miehe et al. 2009, 2015, Tambe and Rawat 2009, Aryal et al. 2014, 2015), we selected palatable and unpalatable plant species for livestock and

treated these plants as grazing indicator species. We standardized the species abundance scores of both surveys using a square-root transformation. We then calculated the weighted average (WA) of these species using the standardized abundances and nominal species attributes (1 for palatable and 2 for unpalatable species). The WA scores for the grazing indicator species in both surveys were used as an explanatory variable in ordination and regression analyses.

#### Quantitative analysis

*Changes in species composition.*—We conducted a correspondence analysis (CA) to analyze the change in species composition over underlying spatial and temporal gradients that were post-hoc fitted to the species space. We extracted the species and site scores of the CA axis that represented the temporal gradient (sampling time) to interpret the temporal change in species composition and its driving factors. We conducted ordination analyses in CANOCO version 5.04 (ter Braak and Šmilauer 2012).

We also conducted a one-way analysis of similarity (ANOSIM) test with Bray-Curtis distance measures (Clarke 1993) to analyze the extent of change in species composition between 1990 and 2014. This analysis is a distance-based non-parametric test of the degree of difference between two or more species groups. A similarity percentage (SIMPER) procedure (Clarke 1993) was used to elucidate the contribution of each species to temporal changes in species composition. We performed ANOSIM and SIMPER in R version 3.4.2 (R Core Team 2017).

*Explanatory factors of the temporal changes.*—Collinearity was detected between the climatic factors ( $r = 0.99$ ). Therefore, instead of using both the climatic variables, we selected only WMT for the analyses. We tested the effect of the climatic and grazing factors on the temporal changes in species composition by treating the interaction between WMT and grazing as a predictor variable and the temporal variation in species composition (CA axis 2) as a response variable in linear regression analyses. We performed regression analyses in R version 3.4.2.

*Shifts in species' elevation optima.*—We used generalized linear modeling with a binomial distribution and a logit link function for estimating the changes in species' elevation optima between

the two surveys, which is a common technique to investigate species relationships along environmental gradients. Here, we used only the species that had significant unimodal responses along the elevation gradient in both surveys.

*Elevational shifts in species assemblages.*—We applied WA regression and calibration technique with the “rioja” package in R version 3.4.2 (Juggins 2016) to analyze elevational shifts in the assemblages of the 61 frequent species that were found in both surveys. Weighted average regression and environmental calibration has been perceived as a theoretically sound, computationally straightforward and robust analytical technique of environmental reconstructions (Birks et al. 1990, 2010). It has also been applied in modern vegetation ecology for quantification of climatic responses of plant communities (e.g., Brady et al. 2010, Bertrand et al. 2011, 2016, De Frenne et al. 2013). In this technique, first WA regression establishes a relationship between historical species composition and an environmental variable in question, and then, this relationship is used to predict the environment for a point with a known species composition (modern dataset), which is called calibration. Using classical and inverse deshrinking techniques of WA (normal WA regression) as well as WA-PLS (partial least squares WA regression) link functions, we searched for the most accurately calibrated elevations for the 2014 sample plots. The difference between the observed and predicted elevations of the 2014 plots was considered as the elevational shift in species composition, where positive values indicate an upslope shift in species composition.

We then developed three linear regression models (null model, model with time + elevation, and model with elevation: time as predictors) to test for elevational shifts in species composition over time. We also selected the palatable and unpalatable species from the full datasets of 1990 (246 species) and 2014 (269 species), and we applied the above-mentioned technique to analyze the elevational shifts in palatable and unpalatable species compositions.

## RESULTS

### Changes in species composition

Correspondence analysis revealed clear changes in species composition in both sites from 1990 to

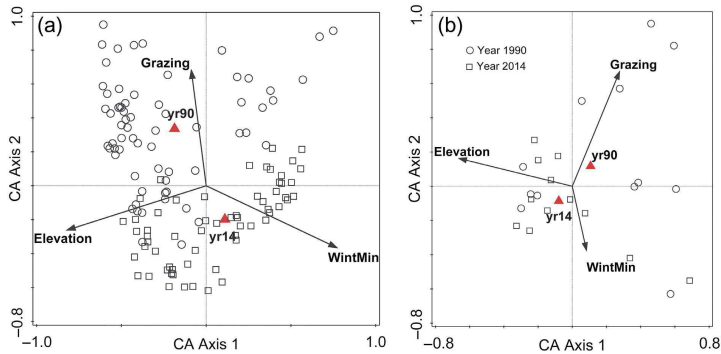


Fig. 2. Correspondence analysis (CA) biplot of Site 1 and Site 2 species compositions with post-hoc fit of supplementary variables to species space: elevation, sampling year (yr90 = year 1990; yr14 = year 2014), mean winter minimum temperature (WintMin), and grazing indicator gradient. (a) Site 1: total variation = 2.40; variance explained by supplementary variables = 19.30%, eigenvalues (axis 1 = 0.40, axis 2 = 0.17). (b) Site 2: total variation = 2.32; variance explained by supplementary variables = 16.4%, eigenvalues (axis 1 = 0.50, axis 2 = 0.29).

2014 (Fig. 2). A post-hoc fit of the explanatory variables to the species space revealed that the variation is explained by the spatial and temporal gradients. In both sites, most of the variation is along the first CA axis, which represented the spatial (elevation) gradient (CA axis 1 vs. elevation,  $r = -0.82$  for Site 1 and  $r = 0.60$  for Site 2) and the temporal climatic factors (Appendix S2: Table S1). The second CA axis for Site 1 is represented by the composite temporal gradient of sampling time ( $r = -0.72$ ) and grazing gradient ( $r = 0.61$ ). Additionally, the temporally estimated WMT also reveals a clear affinity toward the second axis. The second CA axis for Site 2 represents a composite temporal gradient of grazing ( $r = 0.70$ ), time, and climatic factors (Appendix S2: Table S1).

We extracted the species scores of CA axis 2 to further analyze the change in species composition along the temporal gradient. The species with higher negative scores along CA axis 2 mostly increased in frequency from 1990 to 2014 (Appendix S2: Table S2). The overall pattern of temporal change in species composition along the alpine elevation gradient and its potential driving factors are diagrammatically represented in Fig. 3.

The temporal trends revealed by the ordinations are confirmed by the analysis of similarity, which revealed significant differences between

the historical and current species compositions (ANOSIM  $R = 0.39$ ,  $***P = 0.001$  for Site 1, and  $R = 0.19$ ,  $*P = 0.01$  for Site 2). Out of 56 species of Site 1, 33 significantly contribute to the temporal changes and account for over 67% of the temporal differences in species composition. Of these, 31 species significantly increased in abundance and two species decreased in abundance over time (Table 1). Similarly, out of 28 species in Site 2, nine species significantly contribute to the temporal differences and account for over 39% of the observed temporal differences in species composition. Of these, eight species increased in abundance and one species decreased in abundance (Table 1).

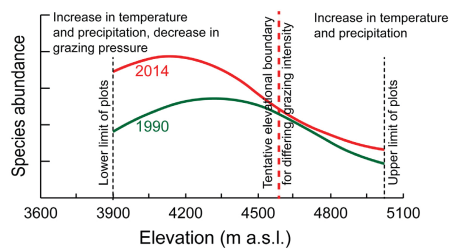


Fig. 3. Diagrammatic presentation of the tentative observed pattern of temporal change in species abundances along the elevation gradient.

Table 1. Summary of the analysis of similarity (Clarke 1993) between species compositions in 1990 and 2014.

Species	Contr (%)	Mean abun (%)		$\Delta$ abun	P-value	Palatability
		1990	2014			
Site 1						
Kobr.nep	3.17	0.09	0.98	0.89	0.001	Palatable
Pleu.hoo	2.48	0.18	0.84	0.66	0.001	Unpalatable
Saus.wer	2.32	0.06	0.73	0.67	0.001	–
Cyan.inc	2.10	0.22	0.73	0.50	0.001	Unpalatable
Kobr.pyg	2.08	0.61	0.10	–0.52	0.001	–
Pote.arg	1.95	0.09	0.63	0.54	0.001	Palatable
Euph.str	1.85	0.25	0.61	0.36	0.001	Unpalatable
Thali.alp	1.76	0.10	0.56	0.46	0.001	Unpalatable
Leon.jac	1.56	0.13	0.50	0.37	0.001	–
Saxi.hof	1.49	0.04	0.45	0.41	0.001	–
Aste fla	1.41	0.07	0.44	0.36	0.001	–
Soro.hoo	1.38	0.06	0.34	0.28	0.001	–
Cyan.lob	1.31	0.15	0.39	0.24	0.001	Unpalatable
Rhod.dis	1.21	0.06	0.37	0.31	0.001	–
Alet.pau	1.20	0.09	0.34	0.25	0.001	Palatable
Gera.don	1.19	0.09	0.35	0.27	0.001	–
Junc.con	1.14	0.07	0.34	0.26	0.001	Palatable
Pote.sin	1.02	0.07	0.27	0.20	0.001	–
Guel.him	0.97	0.09	0.27	0.18	0.001	Palatable
Mori.pol	0.74	0.03	0.23	0.20	0.001	Unpalatable
Pote.ari	0.68	0.04	0.19	0.15	0.001	–
Saxi.ari	0.62	0.04	0.18	0.13	0.001	–
Junc.tri	0.55	0.01	0.16	0.15	0.001	Palatable
Pol.hoo	1.26	0.13	0.37	0.24	0.002	–
Gent.pro	1.82	0.27	0.58	0.31	0.003	–
Mori.nep	1.21	0.13	0.35	0.22	0.003	Unpalatable
Rhodo.le	0.93	0.10	0.23	0.12	0.007	–
Crem.nep	1.87	0.25	0.55	0.29	0.008	–
Dant.cum	0.97	0.10	0.26	0.15	0.019	–
Rhod.coc	1.87	0.57	0.19	–0.37	0.022	–
Anap.mon	0.99	0.10	0.27	0.17	0.029	Palatable
Junc.uni	0.20	0.01	0.05	0.03	0.050	–
Spir.arc	0.70	0.07	0.18	0.10	0.052	–
Site 2						
Leon.jac	4.03	0.17	0.75	0.58	0.003	–
Kobr.nep	4.11	0.25	0.83	0.58	0.008	Palatable
Cyan.lob	3.64	0.17	0.67	0.50	0.008	Unpalatable
Mori.pol	3.36	0.17	0.58	0.42	0.015	Unpalatable
Agro.hoo	2.95	0.08	0.50	0.42	0.016	Palatable
Saxi.par	2.70	0.08	0.42	0.33	0.024	–
Euph.str	3.31	0.25	0.58	0.33	0.080	Unpalatable
Saus.leo	2.74	0.50	0.08	–0.42	0.080	Unpalatable
Mori.nep	2.60	0.17	0.42	0.25	0.090	Unpalatable

Notes: Only the species that significantly contributed (Contr %) to the observed differences between species compositions are listed. Mean abundance of species (Mean abun %); change in mean abundance of species ( $\Delta$ abun). The species abbreviations are listed in Appendix S2: Table S2.

#### Explanatory factors of the temporal changes

In Site 1, an interaction between WMT (AP) and the grazing gradient significantly explains ( $***P = 2.20e-16$ ) the temporal variation in species composition (Fig. 4a; Appendix S3). In Site 2, the

interaction between the climatic factors and the grazing gradient is insignificant. However, the individual factors significantly explain (WMT  $*P = 0.03$ , grazing  $***P = 1.35e-4$ ) the temporal variation in species composition (Fig. 4b, c).



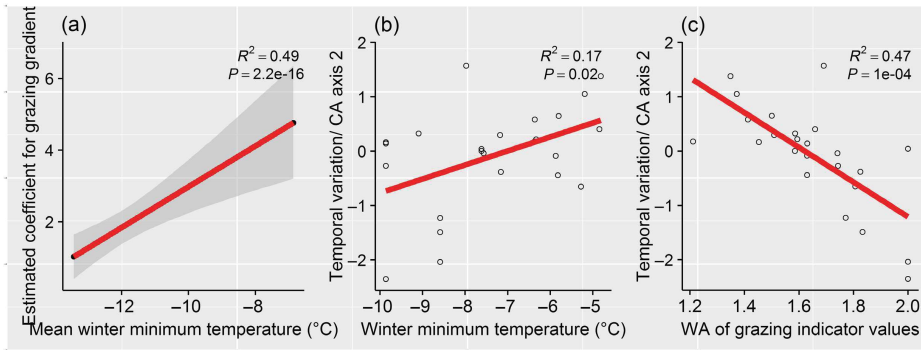


Fig. 4. Linear regression models with temporal changes in species composition (CA axis 2) as a response variable and (a) interaction between mean winter minimum temperature (WMT) and temporal grazing gradient (GR) (weighted average of grazing indicator values) as predictors for Site 1 species composition; and (b) WMT and (c) GR as predictors for Site 2 species composition.

#### Shifts in species' elevation optima

There were 28 species in 2014 and 20 species in 1990 with significant unimodal responses along the elevation gradient. However, only 12 species had unimodal responses in both surveys. Of these, the elevation optima decreased for eight species and increased for four species over time (Table 2).

#### Elevational shifts in species assemblages

The observed elevations of 62 sample plots in 2014 are lower than those predicted from the species compositions and elevations of 1990, whereas 30 plots increased in elevation (Fig. 5a).

These results indicate an overall downward shift of species assemblages during the past 25 yr. Among the three alternative models tested for elevational shifts, the one with interaction between the observed elevation and sampling time was the best model (ANOVA  $***P < 2.2e-16$ ,  $F = 501.75$ ). The significant interaction ( $r^2$  adj. = 0.91,  $***P < 2.2e-16$ ) between the observed elevation and sampling time indicates that although there is a significant downward shift in species assemblages, species at higher elevations, especially above 4700 m a.s.l., are shifted upward (Figs. 3, 5a). The same is true for the unpalatable and palatable species compositions (Fig. 5b, c). For

Table 2. Changes in elevation optima of species between the 1990 and 2014 surveys.

Species	Optima 1990 (m)	Optima 2014 (m)	Change (m)	CI low 1990	CI up 1990	CI low 2014	CI up 2014
Cala.niv	4560.97	4739.36	178.39	-5.19	24.92	11.21	37.1
Cyan.inc	4529.83	4542.41	12.58	-6.54	20.82	4.87	20.7
Cyan.lob	4403.32	4262.03	-141.29	-85.08	-4.49	-16.74	-6.21
Euph.str	4456.02	4402.79	-53.23	-12.47	4.83	-7.77	0.75
Gent.pro	4512.49	4633.18	120.69	-6.67	13.41	8.03	28.2
Guel.him	4459.78	4397.04	-62.74	-62.89	13.84	-18.06	0.58
Kobr.pyg	4747.17	4666.25	-80.92	4.95	27.5	54.53	388.27
Leon.jac	4452.64	4313.04	-139.6	-20.47	6.86	-13.75	-4.37
Mori.nep	4431.62	4391.76	-39.86	-16.87	4.52	-10.83	-0.04
Poly.hoo	4445.72	4432.32	-13.4	-65.27	5.05	-11.75	3.52
Pote.ari	4455.25	4515.96	60.71	-22.3	12.57	-3.5	30.55
Thal.alp	4502.01	4471.65	-30.36	-9.31	16.26	-4.03	6.82

Notes: Non-overlapping 95% confidence intervals of species' elevation optima in 1990 and 2014 indicate a significant elevational shift in optima. CI low and CI up are the lower and upper limits of the 95% confidence interval, respectively.

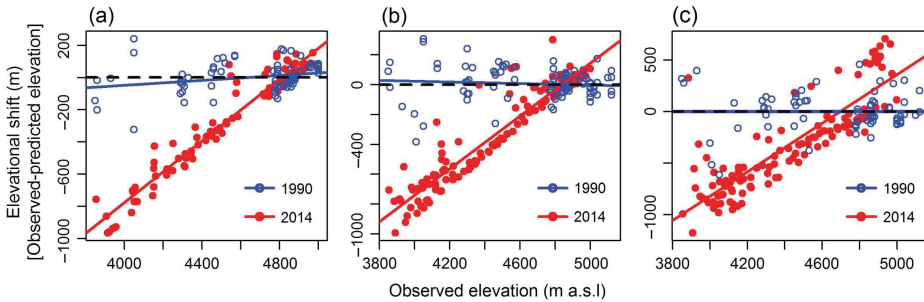


Fig. 5. Changes in the sample plot elevations from 1990 to 2014 based on the composition of the (a) total, (b) unpalatable, and (c) palatable species assemblages. The difference in the observed and predicted elevation of the sample plots gives an estimate of the elevational shift in species assemblages. Positive values of 2014 plots along the  $y$ -axis indicate an upslope shift in species assemblages. The dashed horizontal line is the reference for no change in sample plot elevation.

these species, the regression model with the interaction between the observed elevation and sampling time was the best model among the three models tested (unpalatable: ANOVA  $***P = <2.2e-16$ ,  $F = 499.98$ ; palatable: ANOVA  $***P = <2.2e-16$ ,  $F = 158.35$ ). However, a downward shift was particularly pronounced for the unpalatable species assemblages, and an upward shift at higher elevations was more prominent for palatable species assemblages.

## DISCUSSION

### Changes in species composition

We found significant changes in the species composition of alpine Himalayan plant assemblages from 1990 to 2014, as evidenced by an increase in the frequency, abundance, and downward elevational shifts of species. The changes are significantly explained statistically by temporal trends in climatic factors, especially winter temperature and AP, and a grazing land-use factor. Therefore, our findings partly support both of the hypotheses of climate- and land-use-driven temporal changes in species composition.

The documented changes partly follow the major trends in climate- and land-use-driven compositional changes in other high-elevation areas of the world (e.g., Grabherr et al. 1994, Klanderud and Birks 2003, Walther et al. 2005, Odland et al. 2010, Gottfried et al. 2012). However, our findings are unique in several aspects.

First, our study does not cover the mountain summits because in the central Himalayan region, mountain summits above the alpine belt are permanently capped with ice and snow. Second, the study uses the same set of species from both surveys. Therefore, rather than documenting changes due to the arrival or loss of species, we focus on changes in species that were already recorded in the 1990 survey with  $>3\%$  frequency. Third, rather than studying the effects of individual climatic or land-use factors, we provide evidence that the documented changes are related to the interactions and feedback mechanisms of the spatially and temporally varying climate and land-use regimes in the region.

A temporal increase in WT may enhance early-spring melting of snow and decrease snow cover, which strongly modifies both the physical and thermal environments in alpine areas (Kreyling 2010, Williams et al. 2015). An increase in AP, especially during the monsoon (June–August), enhances water availability and potentially reduces warming-driven water stress during summer (Pfeifer-Meister et al. 2016). Thus, jointly, these climatic factors may result in longer growing seasons with warmer and more humid conditions in the spring and summer. The phenologies of alpine plant species are generally strongly temperature-sensitive. Therefore, the dormancy period of alpine plants will be shortened with an increase in the growing season, which strongly enhances the general fitness and persistence of

plants (Pigliucci and Elizabeth 2001). A rise in WT may also directly enhance the metabolic rate of alpine plants and increase the mineralization of limiting nutrients, such as nitrogen, which can increase primary productivity (see Williams et al. 2015). These changes in climatic factors are uniform along the entire temporal temperature-elevation gradient. Therefore, temporal climate-driven changes in vegetation are expected to be uniform along the elevation gradient. However, one may expect a more pronounced response at lower elevations due to a pronounced temporal change in grazing intensity at lower elevations (see Fig. 3).

Grazing intensity has significantly decreased over recent decades due to declines in livestock populations, especially yaks, sheep, and goats, which are the typical grazers of alpine pastures (Bhatta et al. 2012b, GoN-CBS 2013, Aryal et al. 2014). These livestock graze more frequently in the lower alpine pastures (below ~ 4500 m), and their population reductions have therefore resulted in a more substantial decrease in grazing pressure in the lower alpine region compared to the upper alpine belt. Consequently, typical indicators of intense grazing, which are nitrophilous species in the lower alpine belt, such as *Elsholtzia* spp., *Iris kemaonensis*/l. *goniocarpa*, *Plantago erosa*, *Ranunculus* spp. and *Rumex nepalensis* (sensu Miede et al. 2009, Tambe and Rawat 2009, Aryal et al. 2014), were rare in our study and were therefore removed during data processing. However, partly in agreement with our second hypothesis, the remaining palatable and unpalatable species have increased notably (see Table 1), especially toward the lower elevations. An increase in unpalatable and palatable species together may be due to a lack of competition among the species for resources (space, water, and nitrogen) after reduction of grazing pressure. Thus, increases in WT and AP accompanied by a reduction in the grazing pressure seem to have overall positive effects on alpine plant species composition by resulting in a net increase in resources and a reduction in stress over a longer growing period.

#### *Elevational shift in species assemblages*

Partly refuting our first hypothesis, we observed significant downward shifts in species assemblages, and nearly 70% of the sample plots gained species that were from elevations higher than the actual elevations of the plots. Consequently, the

predicted elevations of most sample plots are higher than their actual elevations, and this trend is more pronounced toward lower elevations. However, species assemblages of the few high-elevation plots have shifted upward over the same time period (Fig. 3). This trend is further supported by downward shifts in the elevation optima of the majority of the analyzed species.

Our finding is generally in line with the study from the western Himalayan region, which documented multidimensional and species-specific responses of plant species to climate change (Dolezal et al. 2016). These changes were likely due to the interactions between climate-driven impacts with increasing precipitation and physical disturbance. However, the observed patterns contrast with a large number of studies from other mountains and alpine areas across the world that documented increases in the elevation optima of species and upslope shifts in species assemblages mainly in response to climate warming (Grabherr et al. 1994, Klanderud and Birks 2003, Lenoir et al. 2008, Gottfried et al. 2012). Most of the studies that documented upslope shifts in species' distributions also reported the opposite trends or no change in elevational distributions for the sizeable minority of species (see Lenoir et al. 2010, Felde et al. 2012). However, these unexpected responses have generally been treated as anomalies and therefore largely ignored (but see Frei et al. 2010, Lenoir et al. 2010, Crimmins et al. 2011). The downslope shifts in species distributions are assumed to be mostly governed by factor(s) other than warming, such as changes in biotic interactions, dispersal limitation of the alpine species, land-use changes, frost and snow cover dynamics, and changes in precipitation patterns and moisture availability (Frei et al. 2010, Lenoir et al. 2010, Crimmins et al. 2011, Felde et al. 2012).

We argue that the observed elevational shifts in species' distributions are most likely the result of mechanisms associated with the interactions between increased WT, increased AP, and decreased grazing pressure in the alpine areas of central Nepal, which is in line with the suggestions in previous studies (Lenoir et al. 2010, Felde et al. 2012, Williams et al. 2015). The thermal and physical stress faced by the majority of species at higher alpine elevations, and simultaneous increases in space, temperature, and water as well

as a decrease in grazing pressure toward the lower alpine belt most likely caused unexpected downhill shifts of the species despite increasing trends in WMT.

In the alpine areas, snow is an effective insulator and a mediator of soil microclimate. Reduced snow cover or earlier snow melt, most likely due to increased WT in the upper alpine regions, can expose soil systems to extreme low temperatures. Soil freezing and frequent frost can lead to both physical and physiological stress for the plant roots (Bokhorst et al. 2011). In addition, there is limited suitable ground for species colonization in the areas above 5000 m. Thus, plant species from the lower alpine belt find neither suitable surfaces nor suitable environmental conditions to further extend their ranges toward higher elevations. In contrast, the atmospheric temperature in the valley bottom (3000–4000 m a.s.l.) remains 2.5–5°C warmer than in the upper alpine areas (4500–5000 m a.s.l.). Consequently, late-winter and early-spring frost and soil freezing are less severe toward lower elevations. Moreover, increased WT may increase the availability of suitable surfaces for species colonization due to early snow and ice melt. Additionally, increased WT provides more energy that enhances plant metabolism. The likely negative effects of warmer temperatures during summer are moderated by increased precipitation (Pfeifer-Meister et al. 2016) and snow melt. Concurrently, reduced grazing pressure makes the lower alpine belt even more suitable for plant colonization and growth. Moreover, grazing- and climate change-induced biotic interactions such as facilitation (but less stress and competition due to increased precipitation and soil nitrogen) in the lower elevation regions likely facilitated the species to expand their populations in these areas (see Lenoir et al. 2010). As a cumulative effect of these interacting factors, populations of the majority of species in the lower alpine belt grow relatively faster than species in the upper alpine belt and expand geographically. Thus, the majority of alpine species shift in frequency toward lower elevations despite a significant increasing trend in winter temperature.

However, typical alpine species at the upper extremes of the alpine belt are well adapted to extreme cold and harsh physical conditions, and they can survive during the winter (Körner

1997). Grazing pressure in these areas remains minimum or non-existent because the livestock rarely reach an elevation above 4600 m. Therefore, the upper alpine species assemblages exhibited an upward shift to track their temperature niche under ongoing climate warming.

## CONCLUSIONS

Our study reveals that the significant change in alpine species composition of the central Himalayan from 1990 to 2014 was most likely driven by interactions of contemporary climate and land-use changes, especially reduced grazing. Although species exhibited individual responses to environmental changes, the vast majority of the species assemblages shifted toward lower elevations, which contrasts with the expected general response of plant species to climate warming. The complex feedback mechanisms and interactions between warmer WT, increased precipitation, reduced grazing pressure, and thereby changed species interactions likely modified the general climatic response of species and facilitated the downslope shift of alpine species assemblages. Climatic and land-use responses of plant species assemblages should therefore be studied focusing on the potential interactions between both the climatic and the land-use factors because such interactions and feedback mechanisms have potential to mask or modify the expected climatic or land-use response of biodiversity.

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