



# Does tree canopy closure moderate the effect of climate warming on plant species composition of temperate Himalayan oak forest?

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## Keywords

Canopy closure; Climate warming; Himalaya; Land-use change; Mesophication; Oak forest; Thermophilization

## Nomenclature

Gurung (1991) for ferns; Press et al. (2000) for flowering plants

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## Abstract

**Question:** We ask if there are significant changes in plant species composition after 20 yr of documented temperature increase (~1 °C), and if the temporal changes are different in closed temperate oak forest compared to semi-open canopy. Answers to these questions may indicate if climate warming and/or canopy closure, controlled by land-use regime, is the main driver of any documented compositional changes in the forest between 1993 and 2013.

**Location:** Phulchoki Mountain, central Himalaya (Nepal).

**Methods:** We resampled 64 plots of 100 m<sup>2</sup> after 20 yr and recorded all terrestrial vascular plants and percentage canopy cover in each sample plot. We analysed the compositional changes in terms of species abundance, frequency and spatial translocation in relation to atmospheric temperature and canopy cover using univariate and multivariate statistics.

**Results:** We find clear changes in the species composition, with abundance of almost half of the studied species having increased and one-quarter of the species having decreased over the past two decades. The changes vary among life forms: trees increased, whereas decreasing species were mainly herbaceous or shrubs. Similarly, shade-tolerant species increased, whereas those adapted to open habitat decreased. The compositional changes are mainly explained through the increased regional temperature, with a significant buffering effect of tree canopy cover. A significant increase in low-elevation (warm-adapted) species is detected, but this thermophilization is only found in the semi-open forest.

**Conclusions:** Fine-scale temporal changes in the temperate oak forests are mainly driven by macroclimate warming, although change in land-use regime also has a profound direct effect by governing canopy closure that, in turn, moderates the effect of climate warming. Tree canopy cover governs the relative abundances of different species based on their adaptive characteristics, such as shade tolerance and life-form traits. The magnitude of the temporal vegetation change would therefore be dependent on both the degree of regional climate warming and forest canopy closure.

## Introduction

Climate and land-use changes are major drivers of vegetation change, leading to transformation of natural landscapes (MEA 2005). Shifts in abundance and distribution patterns of plant species across the globe are now documented for several vegetation types (Gottfried et al. 2012; Newbold et al. 2015). However, precise quantification and

underpinning causation of these vegetation changes over different spatial and temporal scales is always a challenge due to complex interactions of their drivers (MEA 2005; Vetaas et al. 2012). Canopy closure of temperate forests for instance, interacts with macroclimatic warming to moderate its effects on understorey vegetation (De Frenne et al. 2013). Yet it is unclear if this buffering role is influenced by the degree of canopy disturbance in the past, successional

stage of the vegetation and/or life form, adaptive features and habitat preferences of the understorey species.

A majority of researchers attributes up-slope or polewards shifts in plant species ranges to rising atmospheric temperature during recent decades (e.g. Lenoir et al. 2008; Chen et al. 2011; Gottfried et al. 2012), but unexpected down-slope range shifts in a warming climate, or upward shifts irrespective of climate warming, are also occasionally observed (Lenoir et al. 2010a; Grytnes et al. 2014). Moreover, significant time lags in the expected species response to temperature increase have also been reported (e.g. Bertrand et al. 2011; Wu et al. 2015). This disparity in the plant species response to climate warming might be due to a confounding role of land-use change (Lenoir et al. 2010b; Bertrand et al. 2011; Dullinger et al. 2015; Nowacki & Abrams 2015). For instance, ‘thermophilization’, where there is an increase in warm-adapted species and simultaneous decrease in cold-adapted species of temperate forests, often lags behind warming because, concomitant with enhanced temperature, the canopy cover of the forests in some regions is increasing due to changes in land-use regime.

Temperate forests comprise about 16% of the world’s forests (Hansen et al. 2010). These forests have experienced recent climate warming together with other environmental changes, such as alterations to historic disturbance regimes and habitat degradation, and therefore vegetation change is expected to be more acute than for other vegetation types (Lenoir et al. 2010b; Bai et al. 2011; Duguid & Ashton 2013). Several studies of temperate forests across Europe and North America have found significant temporal changes in the herbaceous vegetation over recent years. These vegetation changes have been attributed to land-use changes, such as logging intensity and fire suppression (Nowacki & Abrams 2008, 2015), and to environmental changes such as herbivory (e.g. Côté et al. 2004), acidification or eutrophication and climatic change (e.g. Thimonier et al. 1994; Verheyen et al. 2012 and reviewed therein; De Frenne et al. 2013; Dullinger et al. 2015; Pederson et al. 2015). However, comparative studies of plant community change in lower-mountain forests in response to recent climate and land-use change (leading to forest canopy closure) are scarce in comparison to those in high-elevation vegetation. This is even more so in Asia, where long-term studies of temperate vegetation change are very scarce (but see Bai et al. 2011; Yu & Sun 2013) and the effect of macroclimatic warming coupled with a denser canopy on forest species composition has rarely been discussed.

Alongside the regional temperature increase, many temperate forests have become denser due to reduced land-use intensity (e.g. forest management or changes in disturbance regimes such as fire suppression) (Nowacki &

Abrams 2008, 2015). With increasing canopy closure, the forest microclimate is increasingly protected from direct solar radiation and has lower maximum temperatures and increased humidity, a phenomenon termed ‘mesophication’ (sensu Nowacki & Abrams 2008). The overall effect is uncertain, but most likely canopy closure may counteract the effects of macroclimate warming on the forest understorey (De Frenne et al. 2013; Nowacki & Abrams 2015). Canopy cover directly or indirectly governs development and distribution of understorey vegetation by regulating understorey light and soil conditions (Chen et al. 1999; Bartels & Chen 2010; Verheyen et al. 2012). Consequently, the effect of enhanced temperature is likely to be difficult to disentangle from changes driven by stand development and canopy closure, and the potential responses to climate warming may easily be masked, modified or buffered (Lenoir et al. 2010b; De Frenne et al. 2013; Abrams & Nowacki 2015).

This trend of rising global temperature and canopy closure is manifest in the temperate forests of the central Himalaya. After decades (1970–1990) of exploitation of oak forests for cattle fodder, timber and firewood (Shrestha et al. 2012a), new forest regulation has led to enhanced forest cover locally as well as regionally (Pokharel et al. 2007). At the same time, regional atmospheric temperature has significantly increased, although climate change in Nepal is rather heterogeneous (Shrestha et al. 2012b).

This study is based on a re-survey of species composition in a temperate oak forest, which was previously sampled in 1993 (Vetaas 1997). Using the same sampling protocols, we investigate the consequences of increased temperature and land-use change on species composition in two proximate sites. Both sites have experienced a significant rise in temperature, but one site has had a dense and stable canopy cover throughout, whereas the other site has experienced increasing canopy cover over recent years.

The main question posed is: are there significant changes in species composition from 1993 to 2013 that may be attributed to increased temperature and/or land-use change (increasing canopy closure)? If changes are documented, we investigate plausible causal links by testing the following hypotheses:

*The climate hypothesis:* Due to climate warming, species with higher temperature optima are increasing, whereas species with lower temperature optima are decreasing. This thermophilization process is expected to be more pronounced under a more open tree canopy than under a closed forest canopy.

*The land-use hypothesis:* Due to increasing canopy closure, shade-tolerant species are increasing, whereas shade-intolerant species (those adapted to open habitats) are decreasing. Decreases in shade-intolerant

species should be more pronounced at the open site due to canopy closing processes whereas the other site has had a closed canopy during both investigations.

We use differences in species composition and the ecological attributes of the species to interpret the causes of any differences found. The two main hypotheses are not mutually exclusive because the two factors, temperature and land-use change, may act concurrently.

## Methods

### Study area

Our study area, Phulchoki Mountain (27°34' N, 85°23' E) lies on the south-eastern periphery of the Kathmandu valley, central Nepal (Fig. 1). It is a part of the montane sub-Himalayan range and falls within the zone of temperate monsoon climate, where 80% of total annual precipitation (about 1900 mm) falls during Jun–Sept, and snowfall is common during winter months (Kansakar et al. 2004). Average monthly temperatures recorded from the nearest weather station range from 18.6–6.7 °C (winter) to 25.2–16.1 °C (summer). The region has experienced a significant rise in mean annual temperature over the past five decades, with an annual warming rate of ~0.05 °C (Fig. 2). Annual rainfall in the region shows no significant trend over the same period (Appendix S1a–f). The studied forests consist of oak–laurel associations common in the subtropical/temperate bioclimatic zone between latitudes 25° and 40°, which cover an elevation belt between ~1000 and 3000 m a.s.l. in the Himalaya (Olson & Dinerstein 1998). The study area (2200–2700 m a.s.l.) harbours *Quercus lanata* and *Q. semecarpifolia* at lower and higher elevations, respectively. Sub-canopy trees such as *Ilex dipyrrena*, *Lindera pulcherrima* and *Rhododendron arboreum* are also associated with the oaks.

### Past and present land-use regime

The first investigation (Vetaas 1997) surveyed six disturbance categories along a land-use gradient in the two sites, but today the two sites can be broadly categorized into two classes: (1) undisturbed forest in the closed site (2600–2700 m) with a closed canopy of mature oak stands, no sign of lopping and sparse ground vegetation; and (2) intermediate disturbance forest of the open site (2250–2450 m) with a more open canopy, signs of lopping in the trees and a denser ground layer vegetation. Although the forest in the open site is now classified as 'intermediately disturbed', it has experienced secondary succession from relatively open forest in 1993 (Vetaas 1997) to more closed canopy at present. Here, increases in temperature and canopy cover are simultaneous, and thus the directional

changes in species composition are expected to be more prominent.

### Field sampling

We traced the plots (32 plots of 10 × 10 m in each site) that had been sampled in 1993, with reference to hand-drawn location maps, elevational records of plots (2200–2700 m a.s.l.) and physiographic notes of Vetaas (1997). Following the sampling technique of Vetaas (1997), we included a single mature oak tree in the centre of each plot and recorded all vascular plants in four subplots (5 × 5 m), which produced an abundance scale of 0 to 4, depending on the occurrence of species in the subplots. Taxonomy follows Gurung (1991) and Press et al. (2000; www.efloras.org), which also provide information on life form (herb, shrub, tree, climber, bamboo) for each species. We measured elevation with a GPS reader (Garmin eTrex10) and canopy cover (percentage) from the centre of each sample plot. Canopy cover is a mean value of the canopy percentage individually estimated by three different people.

### Data analysis

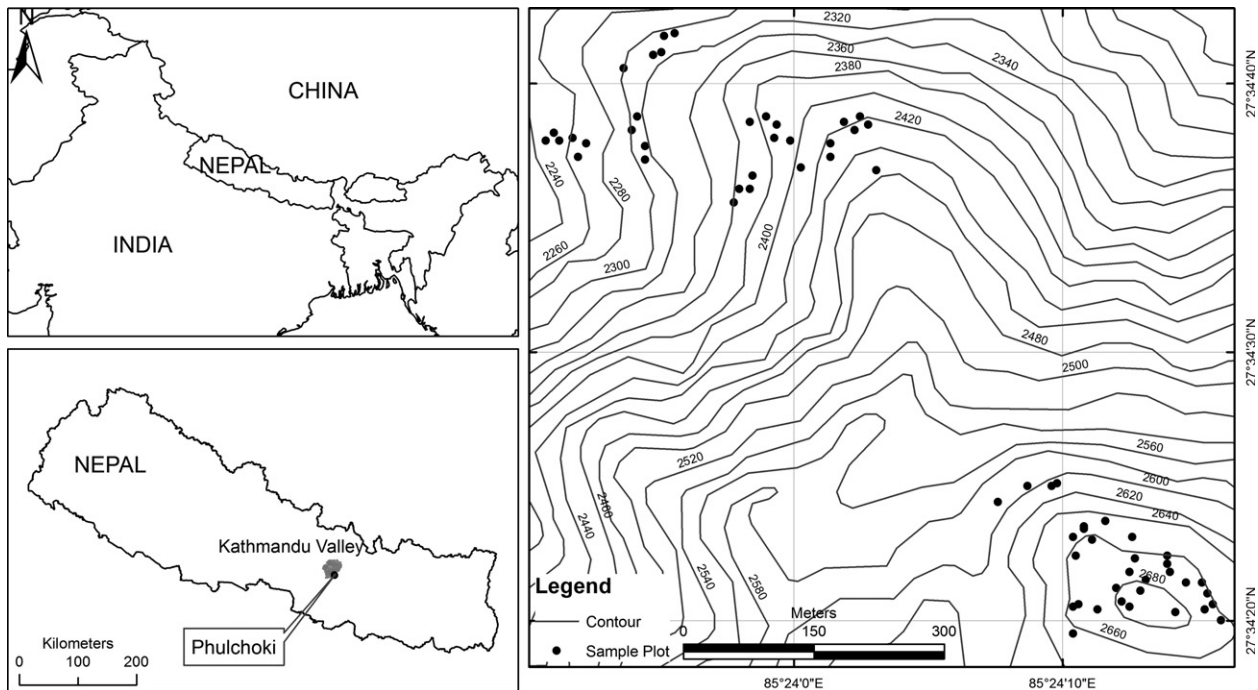
There is always a risk of confounding temporal changes with changes related to differences in each observer's expertise and the nature of plant censuses (Archaux et al. 2006). To minimize such bias in our analyses, we only included species that were common to both surveys, and were with more than two occurrences in either sampling year.

#### Atmospheric temperature

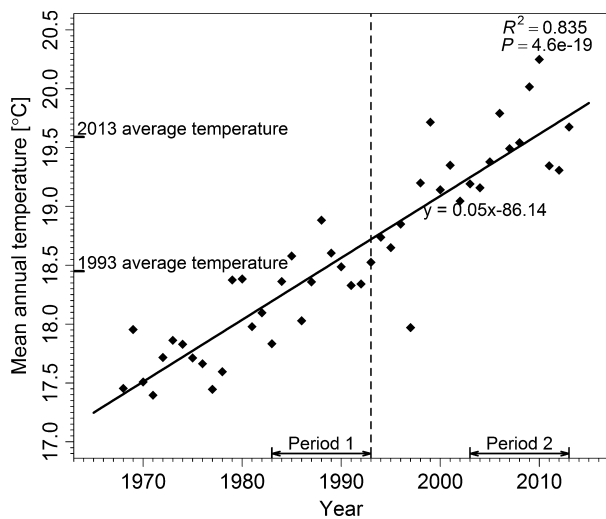
We calculated a 10-yr mean annual temperature ending in 1993 (1984–1993) and 2013 (2004–2013) from the nearest (~5 km N of the study site) climate station (Kathmandu Airport/1030B; at 1337 m a.s.l.; unpubl data from the Department of Hydrology and Meteorology, Nepal). These two temperatures were used to estimate the atmospheric temperature of the sampling plots for the 1993 and 2013 studies using the national lapse rate (0.51 °C decline per 100 m increase in elevation) for Nepal (Dobremez 1976).

#### Weighted average (WA) elevation of sample plots and species

To estimate the overall elevational translocation of the species, we treated species abundance (0–4) as weight and used the elevation range mid-point of the species in central Nepal (Press et al. 2000) to estimate WA elevation of sample plots, and used the elevation of each species' occurrence to estimate WA elevation (elevation optimum) for



**Fig. 1.** Maps showing the location of the study area. The open canopy site (ca 2250–2450 m a.s.l.) is the cluster of plots in the top-left corner of the right-hand map, and the closed canopy site (ca 2550–2700 m a.s.l.) is the cluster of plots in the bottom-right corner.



**Fig. 2.** Linear regression model showing the trend of mean annual temperature from 1968–2013 ( $N = 46$ ). The dated 'plot' temperatures on the left of the plot are based on mean annual temperatures of the previous 10 yr ending in 1993 (period 1) and 2013 (period 2).

the species. A decrease or increase in WA elevation of the sample plots would relate to a respective increase or decrease in the elevation optimum (increase or decrease in temperature optimum) of the species. If warming temperature is a major driver of compositional change, we would

expect lower WA elevation optima (= higher temperature optima) for those species with increased abundances but not for those with decreased abundances (cf. Gottfried et al. 2012).

### Statistical analyses

We analysed the overall change in species composition and approximated the underlying environmental gradients using detrended correspondence analysis (DCA) of the full data sets.

Because there is a profound effect of elevation on the species composition, we attempted to disentangle the effects of temporal and spatial gradients by treating elevation as a co-variable in a partial redundancy analysis (pRDA). pRDA uses absolute values and performs well when the gradient length of the main DCA axes are  $< 2$  SD units (Microcomputer Power, Ithaca, NY, US). RDA uses a co-variance matrix and emphasizes the differences in cover (ter Braak & Prentice 1988). We treated life-form categories and temperature and shade adaptations of each species as supplementary variables, and used canopy cover and atmospheric temperature as test variables in the pRDA. We performed a permutation test with forward selection to test if the considered environmental factors were significant in governing the temporal compositional



changes. All ordination analyses were performed in CANOCO 5.0 (Microcomputer Power).

We applied constrained ordination species scores along the temporal gradient to explore the change in species abundance. The first pRDA axis represents the temporal gradient and we therefore ranked the species scores along this axis to assess their abundance change over the time period. We also performed a rank correlation using R 3.2.2 (R Foundation for Statistical Computing, Vienna, AT) to check if the change in species abundance along the temporal gradient is in accordance with change in their frequencies of occurrences.

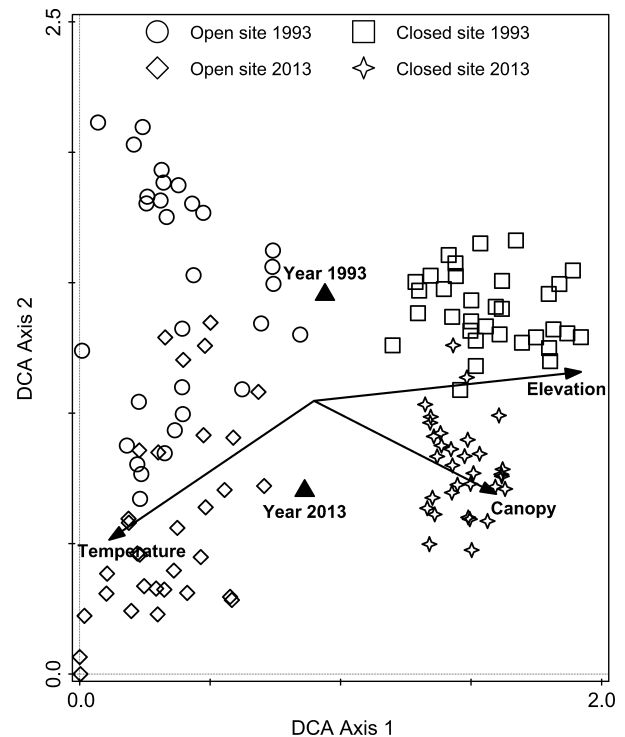
To test if the WA elevations of sample plots differ significantly as per canopy closure, sampling sites and time period, we treated these factors and their interactions as predictors, and WA elevation of sample plot as the response variable in a linear regression model. In a second linear regression model, we tested if there were significant changes in species abundance (pRDA axis 1 species scores) as per species' temperature adaptation, optimum elevation change, shade tolerance and their interactions. The regression analyses were performed in R 3.2.2.

**Results**

**Temporal and spatial gradients of species composition**

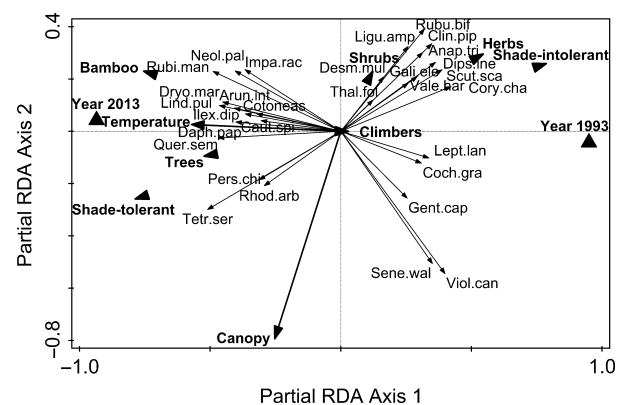
The DCA reveals both spatial and temporal changes in species composition. Plots from the closed canopy site cluster towards the right of the ordination diagram, whereas those from the open canopy site are grouped towards the left, and plots from 2013 have lower scores on the second DCA axis compared to those of 1993 (Fig. 3). A *post-hoc* fit of environmental factors in species space shows that the first DCA axis represents a composite gradient of elevation ( $r = 0.93, P < 0.001$ ), canopy cover ( $r = 0.60, P < 0.001$ ) and temperature ( $r = -0.75, P < 0.001$ ); whereas the second axis is exclusively represented by a temporal gradient ( $r = -0.76, P < 0.001$ ). Nonetheless, both the temperature and canopy cover also show affinity towards the second axis (Appendix S2). All the environmental variables explain about 24% of the total variation in the data set. A rank randomization test (Mann-Whitney U) of the average plot weights in DCA indicates that the overall species abundance has increased significantly ( $Z = -3.93, P < 0.001$ ) between 1993 and 2013 (Appendix S3).

To disentangle the effect of atmospheric temperature and canopy cover while minimizing the effect of elevation (spatial gradient) on the observed vegetation changes, we performed partial RDA (pRDA), treating 'elevation' as a co-variable. This reveals both temperature and canopy cover as significant factors of variation in species abundance. Temporal temperature along the first pRDA axis accounts for 9.5% of



**Fig. 3.** Detrended correspondence analysis (DCA) biplot of combined data sets with *post-hoc* fit of environmental variables and sampling year to species space. Where temperature = 'temporal temperature'/atmospheric temperature of 1993 and 2013 plots, canopy = percentage canopy cover of the sample plots, and elevation = elevation (m a.s.l.) of the sample plots.

the total 14% explained variation, whereas the effect of canopy cover is comparatively weaker (4.5%) along the second pRDA axis (Fig. 4, Appendix S4a).



**Fig. 4.** Partial redundancy analysis (pRDA) biplot of the combined data set constrained by atmospheric temperature (temperature) and canopy cover (canopy), with 'elevation' (m a.s.l.) of sample plots as a co-variable. The life-form categories (herbs, shrubs, climbers, trees, bamboo), shade tolerance (shade-tolerant and shade-intolerant) and sampling year (1993 and 2013) are *post-hoc* fitted as supplementary variables.

The dominance of temporal temperature in explaining variance in the species composition is consistent in the separate pRDA analyses for each location (Appendix S4b–d).

Change in species composition along the first pRDA axis is largely consistent with that along the second DCA axis, because the first pRDA axis represents a temporal gradient (pRDA axis1 vs year,  $r = -0.88$ ,  $P < 0.001$ ) (Appendix S4a). When ranking all the species along the first pRDA axis, the species with higher negative scores increased, those with higher positive scores declined, and those having scores equal to or near to zero have maintained their abundance unchanged over the time period. Out of the 77 species analysed, 35 species have notably increased, 22 species have declined and 20 species have maintained their abundance (Appendix S5). Of the 35 increasing species, nearly 86% are shade-tolerant and 14% are shade-intolerant; whereas, of the 22 decreasing species, 32% are shade-tolerant and 68% are shade-intolerant. Change in the frequency of the species between 1993 and 2013 is largely consistent with change in the abundance of the individual species ( $r_s = -0.90$ ,  $P < 0.001$ ).

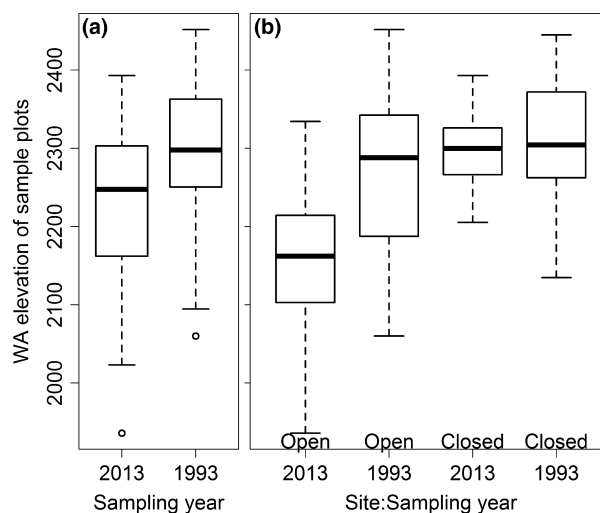
The abundance of most of the tree species, such as *Lindera pulcherrima* and *Neolitsea pallens*, has increased, whereas the abundance of herbs, such as *Dipsacus inermis* and *Ligularia amplexicaulis*, has declined significantly over the time period. As expected, shade-tolerant species have increased and light-demanding herbs of the disturbed canopy have decreased along the gradient of canopy cover (Fig. 4, Appendix S5).

The multiple linear regression analysis reveals a significant decrease ( $t = 8.84$ ,  $P = 0.004$ ) in the weighted average (WA) elevation of the 2013 sample plots compared to the 1993 plots (Fig. 5a). However, the trend is not consistent between the sites. The decrease in WA elevation is significant ( $t = 5.00$ ,  $P < 0.001$ ) only in the open site plots (Fig. 5b). In the multiple linear regression analysis of the change in species abundance, we find a significant increase ( $t = -2.03$ ,  $P < 0.04$ ) in abundance of warm-adapted species and a decline of cold-adapted species (Appendix S6a). Similarly, elevation optima of the increasing species have also significantly increased ( $t = -3.10$ ,  $P = 0.002$ , Appendix S6b). There is a significant increase ( $t = -2.60$ ,  $P = 0.01$ ) in the abundance of shade-tolerant species, with a decline in the abundance of shade-intolerant species (Appendix S6c).

## Discussion

### Changes in species composition

We find significant compositional changes in terms of species abundance, frequency and spatial translocation,



**Fig. 5.** Weighted average (WA) elevation (species abundance as weight) of the sample plots for both sampling years and locations ( $N = 123$ ). (a) WA elevation of sample plots for both sampling years; (b) WA elevation of sample plots in open-canopy and closed-canopy sites for both sampling years. WA elevation of the sample plots is based on mid-points of the elevation ranges of the species for central Nepal (Press et al. 2000). Lower WA elevations of the 2013 sample plots indicate an increase in abundance of species with lower elevation optima (warm-adapted species/species with higher temperature optima) in the sample plots.

where almost half of the species have increased and one-quarter of the species have declined over the past two decades. Most of the tree species increased, whereas the majority of the herbaceous and shrub species declined during the period. Closer examination of the documented ecological changes provides evidence that these are related to the species' macroclimatic requirements as well as to land-use factors, and reflect some of the major trends of temperature and/or land-use-driven changes in temperate forests across Asia and Europe (e.g. Bai et al. 2011; Verheyen et al. 2012; De Frenne et al. 2013; Maclean et al. 2015).

Although our study is not based on a plot-to-plot comparison, the ordination analyses of the resurvey reveal significant systematic changes with respect to composition and life form that may facilitate interpretation of the temporal changes (Ross et al. 2010; Kopecký & Macek 2015). The proportion of total variation explained by temporal increase in temperature and canopy cover is small, but this is inevitable with plant community data that are typically full of noise (Legendre 1993; Økland 1999). In addition, confounding factors make causal interpretation difficult (van der Maarel 1988; Ross et al. 2010; Vetaas et al. 2012). However, partial RDA is able to eliminate confounding spatial factors such as elevation and explain a low but ecologically meaningful variation

with increased temperature (9.5%) and canopy closure (4.5%).

### Climate hypothesis

A temperature increase of 1 °C corresponds to an elevational translocation of ca. 200 m, which is reflected by a change in species composition and species' elevational position (cf. Bertrand et al. 2011). The compositional change revealed that the abundances of warm-adapted species have increased and cold-adapted species have decreased significantly. This apparent temperature-driven compositional change, i.e. 'thermophilization', is in line with several earlier studies on plant species' responses to climate warming across Asia (Bai et al. 2011) and Europe (Lenoir et al. 2010b; Gottfried et al. 2012; De Frenne et al. 2013). This is most probably related to enhanced temperature because there is no significant temporal trend in precipitation, although the increased forest canopy has an indirect effect on microclimate by enhancing moisture retention in the sub-canopy environment, i.e. 'mesophication' (sensu Nowacki & Abrams 2008).

Species in both sites respond to temperature changes, but canopy is a significant factor only in the closed-canopy site by moderating the temperature-driven changes. This is verified by changes in the estimated weighted-average 'plot elevation', which reveal that an up-slope translocation of species is only evident in the open-canopy site, but not the closed-canopy site. This is probably because the dense canopy and sub-canopy in the closed-canopy site may have modulated the process of thermophilization by maintaining a cooler understorey microclimate. Our findings thus provide evidence that cooler microclimates maintained by canopy closure may buffer the effects of climate change on plant assemblages, and therefore, for species threatened by increasing temperature they may act as a potential refugia for some time. This is in line with several studies that have documented the buffering role of canopy closure against the effect of enhanced air temperature at a macroscale (Nowacki & Abrams 2008; Lenoir et al. 2010b; De Frenne et al. 2013). A study from Maclean et al. (2015) has also demonstrated that the thermophilization of a grassland plant community was higher in areas with higher insolation than those with lower insolation. The reasons why plant species' responses to warmer climate are buffered by the presence of cooler microclimates are less straightforward to explain, especially in our study that does not quantify temporal changes in fine-scale temperature. However, a possible explanation is that cooler microclimates often experience less warming and smaller diurnal temperature fluctuations, and are therefore more resilient

to long-term temperature change (Ashcroft et al. 2009; Maclean et al. 2015).

Several microclimate parameters may also differ between the two types of forest canopy. Closed forest can moderate the maximum temperature but may enhance the minimum temperature as well as moisture conditions (Chen et al. 1999; Norris et al. 2012). The densified canopy and sub-canopy layer may affect the understorey by trapping infrared radiation and water vapour released from evapotranspiration, and also by lowering wind speeds (reducing drying effect) thereby allowing higher understorey humidity to prevail (Nowacki & Abrams 2008).

### Land-use hypothesis

The studied forest is an example of a global trend in land-use change that has led to increased closure of canopies in the temperate forest. This may initiate structural changes in microenvironmental conditions, i.e. 'mesophication' (sensu Nowacki & Abrams 2008), thereby influencing the local abundance of species (Nowacki & Abrams 2008; Lenoir et al. 2010b; Verheyen et al. 2012; De Frenne et al. 2013). Canopy cover is a significant explanatory variable in analyses on the combined sites even when elevation is a co-variable, indicating that small-scale variation in the canopy is significant. It has caused an increase of shade-tolerant trees and bamboos and a decline in the shade-intolerant (open habitat-adapted) herbaceous and shrub species. Shade-tolerant species comprise about 86% of the total increased species, and shade-intolerant species comprise 68% of the total decreased species. These changes are similar to the general trend of temperate forest cover-driven vegetation changes across Europe (Verheyen et al. 2012; Nieto-Lugilde et al. 2014). Rapid re-growth of the forest canopy altered both resource quantity and resource heterogeneity on the forest floor to influence the understorey species (Bartels & Chen 2010; Verheyen et al. 2012; Yu & Sun 2013). A negative performance of shade-intolerant species to increased canopy cover indicates that forecasts of climate-related range shifts for understorey species may be modified by tree cover dynamics (Nieto-Lugilde et al. 2014).

The changes may also be partly associated with the life-cycle pattern, environmental sensitivity and dispersal limitations of the species. Trees have longer life spans, delaying their reaction to altered environmental conditions. In contrast, understorey vegetation in temperate forests has shorter generation times and high habitat specificity, and often reacts more quickly to environmental changes (Bai et al. 2011; Duguid & Ashton 2013). However, the majority of the temperate forest understorey species are also expected to be

unable to track climate warming due to profound migration lags that are often influenced by habitat fragmentation (Dullinger et al. 2015). Therefore, a general pattern for all species in response to climate warming cannot be expected, especially in the presence of land-use change as an interacting driver (Bertrand et al. 2011; De Frenne et al. 2013). Although temperature strongly controls the elevational limits of tree species, dispersal lag has also been observed for many widespread forest species (Svenning et al. 2008). Furthermore, our study area is located near the peak of a mountain, at about 2700 m, which may have limited the long-distance immigration of tree species despite the warmer temperature, especially in the site with a closed canopy.

We conclude that regional climate warming mostly drives fine-scale temporal changes in the temperate oak forests of the central Himalaya, but that forest canopy closure may act as a buffer against the effect of warming climate to modify the temporal changes in species composition. Because the individual plant species can exploit fine-scale climatic heterogeneity as a buffer against the effects of macroclimate warming, the magnitude of the temporal vegetation change would be dependent on the intensity as well as the frequency of both regional climate warming and forest canopy closure.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Temporal patterns of rainfall in the Kathmandu valley during 1968–2010.

**Appendix S2.** DCA statistics of the combined data set with the *post-hoc* fit of environmental variables.

**Appendix S3.** Total weight (sample plot score in DCA) of the sample plots in the two sampling years.

**Appendix S4.** Partial RDA (elevation as a co-variable) of the combined data set.

**Appendix S5.** Change in species abundance between 1993 and 2013.

**Appendix S6.** Temporal change in species abundance (pRDA axis 1 species scores).