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Impacts of anthropogenic disturbances on forest succession in the mid-montane forests of Central Himalaya

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Abstract We studied the influence of anthropogenic drivers on the distribution and regeneration of tree species in vegetation at different stages of succession from grasslands to oak forests in mid-montane Central Himalaya. We found fire, grazing, and lopping as the main factors hindering a progressive successional regime towards a late-successional oak community. Succession was studied in five vegetation formations (grasslands, pine, pine–oak, open oak, and dense oak), with similar site conditions, representing a theoretical successional sequence from early- to late-successional stages. A structured survey with uniform distribution of sampling plots in the five selected vegetation formations was conducted to gather information abut the vegetation communities. Early-successional grasslands and pine forests were found to harbour high densities of pine and oak seedling and sapling regeneration. However, recurring fires and chronic unsustainable levels of grazing in these vegetation formations obstructed progressive succession by eliminating regenerating seedling and saplings from the forest understorey. Similarly, in intermediate- and late-successional stages (including pine–oak, open oak, and dense oak), overexploitation of existing oaks trees via lopping and grazing of regenerating oak seedlings and saplings hampered oak regeneration and development. The possibility to convert pine forests into oak as well as the conservation of existing oak forests through controlled grazing and lopping are management options that can contribute to an enhanced functioning of forest ecosystems in the study area. We conclude that with strategic management that restricts the current anthropogenic disturbances, the extent of oak forest in the study area can be increased.

Keywords Succession · Forest fire · Grazing · Lopping · Himalaya · Oak

Introduction

Successional dynamics of forests ecosystems are intricately linked to the supply of ecosystem services

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(ES) that govern the our social, ecological, and economic well-being (MEA 2005; Newcome et al. 2005), especially in coupled human–environment systems where people and nature interact to create a complex feedback mechanism (Liu et al. 2007). Therefore, from the perspective of management of forests for ES, knowledge of successional dynamics and its drivers is essential.

Vegetation communities around the world have been affected by anthropogenic disturbances for millennia (e.g. Bond et al. 2005; Perry and Millington 2008) causing changes in vegetation structure and composition and leading to different successional trajectories. Landscapes that experience chronic disturbances like intensive grazing and forest fires are often maintained in a steady, arrested successional stage, where ecological processes underlying dynamics are either inhibited or weakened (Ghazoul and Sheil 2010). However, being in a steady state over a period of time does not mean that forest ecosystems cannot redevelop into a pre-disturbance stage in the absence of disturbances. Forests are inherently dynamic adaptive systems that have the resilient capacity to maintain ecosystem functioning in the event of external disturbances (Messier et al. 2013) provided they are given the necessary time to recover.

Forests of the central Himalayas are an example of such forested landscapes that have been frequently disturbed over the past few centuries (Tucker 1982; Kumar et al. 2009; Makino 2011). Commercial utilization of forests for timber (until late 1980s) (Semwal et al. 2007), small-scale chronic biomass extraction by the local community (Makino 2011), forest fires (Kumar et al. 2013) and conversion of forests into agriculture lands (Singh and Singh 1992) have contributed to forest degradation in the Himalayas, to various degrees. Chronic disturbances play a strong role in shaping the vegetation structure and composition of these forests (Kumar et al. 2009; Khali and Bhatt 2014; Wangchuk et al. 2014) creating a mosaic of early- and late-successional communities. Most of these disturbances originate from resource use practices adopted by the local population for obtaining necessary products from the landscape (Buffum et al. 2009; Makino 2011; Arya et al. 2012; Singh and Rawat 2012).

This study focuses on the mid-montane Central Himalayan forests between 1500 and 2000 where pine and oak forests occur either as separate vegetation formations or as a conifer-broadleaf mixed forest (Champion and Seth 1968). A theoretical successional sequence in the region should ideally begin with early-successional grassland and pine forests, followed by a mid-successional pine and oak mixed forest community, and ending with a late-successional pure oak forest (Naudiyal and Schmerbeck 2017).

In the mid-montane Central Himalayan region, late-successional oak forests are typically associated with higher contribution to the provisioning, supporting, and regulating ecosystem services, as compared to the early-successional vegetation formations like pine. Joshi and Negi (2011) in a quantitative comparative study on ecosystem services from pine and oak forests clearly highlight the relatively higher importance of oak forests for both provisioning and regulating ecosystem services. A progressive successional dynamic of the current degenerated forests towards the late-successional community is therefore beneficial for the needs of the local population as well as the overall ecosystem functioning.

While theoretically the change in vegetation from a pioneer to late-successional community seems plausible, these dynamics are affected by chronic disturbances at every step of the successional gradient. The aim of our study was to understand the current successional dynamics of the Central Himalayan (CH) forests and highlight the potential of the vegetation formations to develop out of their current arrested stages of succession in the absence of disturbance.

We hypothesize that forests in central Himalaya are maintained in their current state by chronic anthropogenic disturbances and a reduction in disturbance pressure would allow the vegetation communities to move towards a late-successional community. In order to substantiate this hypothesis, the study focuses on answering two questions: (1) What is the current state of successional development in the selected vegetation formations? and (2) How are anthropogenic disturbances affecting the growth, development, and succession in vegetation communities?

Methods

Study area

The study area lies in Dehradun and Tehri Garhwal districts of India, between 30°7′8.817″N to 30°37′40.576″N latitude and 78°31′40.706″E to 77°52′40.423″E longitude (Fig. 1). The forests consist primarily of *Pinus roxburghii* and *Quercus leucotrichophora* along with other interspersed tree species including *Shorea robusta, Cupressus torulosa, Rhododendron arboreum, Quercus floribunda, Cedurus deodara, and Litsea umbrosa* among others (Champion and Seth 1968; Singh and Singh 1992).

More than 90% of the population in the study area is living in a rural setting, where their livelihood has been dependent on forest-based resources for generations (Sandhu and Sandhu 2015). The economy is primarily based on agro-pastoralism (Rao and Pant 2001; Sarin 2001) with approximately 16% of the total area under cultivation (Singh and Singh 1992). Almost all households possess cattle—for fulfilling household needs of milk or dairy—a few or large herds, respectively, of goat, sheep, or buffalo (Semwal et al. 2007).

The management approach followed by the state forest department in the study area is majorly focussed on protection, with a blanket ban on tree felling (Baland et al. 2010). In a bid to enhance participatory forest management, the state forest department of Uttarakhand has encouraged numerous villages to form village-level forest governance bodies called '*van panchayats*' (Baland et al. 2010). Today, there are more than 12,000 *van panchayats* across the state. However, their control over forest management has been significantly curbed since their inception. These institutions lack administrative and financial autonomy and all management decisions made by *van panchayat* need to be approved by the divisional forest officer of the state forest department (Sarin 2001; Negi et al. 2012). However, on an informal level forest ecosystem dynamics is managed through grazing, lopping, and collection of litter and coarse woody debris by the local population to meet there daily household needs. Apart from that, forest fires, often driven by the desire to generate fresh grasses for fodder, play a major role in maintaining the forest

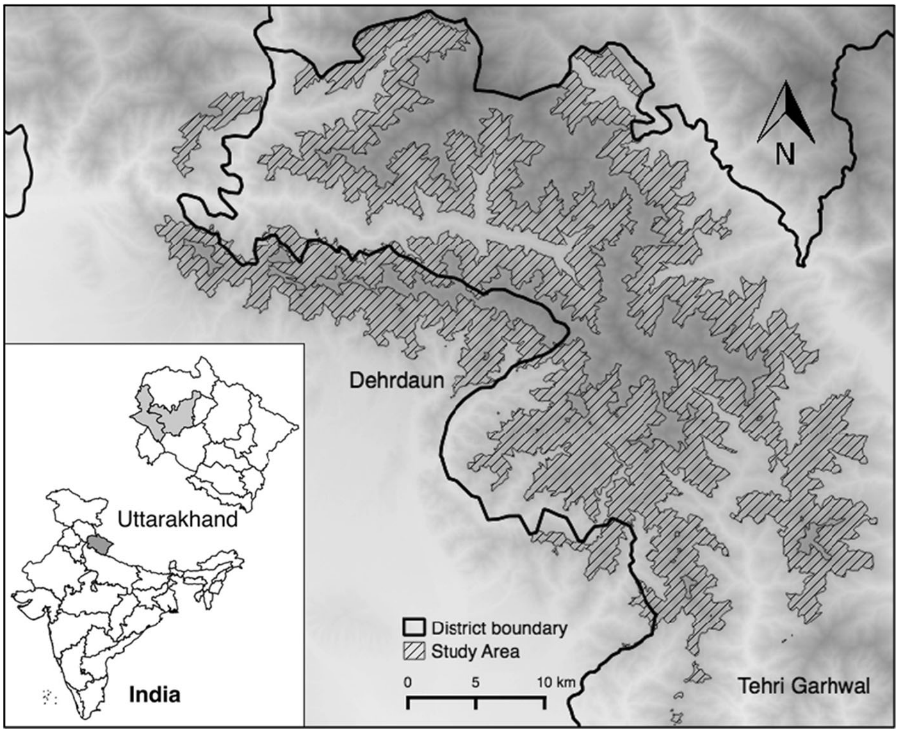

Fig. 1 Location of study area

dynamics in the study area. Grazing, lopping, collection, and fire therefore act as informal, yet the most intensive forms of management that the study area faces at the moment.

Data collection

Since natural ecological succession can span over a period of hundreds of years (Walker and Wardle 2014), this study employed a chronosequence approach that involved a time series of vegetation stands in different age classes to capture successional dynamics in the limited timeframe of this study. Due to a lack of long-term data, this study takes inspiration from the chronosequence method that involves studying an unreal time series of vegetation formations in different age classes (Aide et al. 2000; Ruiz et al. 2005) to analyse successional dynamics. Therefore, five vegetation formations (grassland, pine, pine–oak, open oak, dense oak) representing likely stages in a successional sequence, from early- to late-successional community were selected based on existing ecological knowledge (see Naudiyal and Schmerbeck 2017).

The criterion for selection of the study area was that all five vegetation formations being assessed should be adequately represented under similar site conditions. Similarity in site conditions is essential to arrive at any credible conclusions about vegetation communities, by reducing biases that might arise due to dissimilarities in site conditions in the sampling sites.

The parameters maintained across all sites were slope (20°–30°), elevation (1500–2000 m), and geology (Mussoorie group). Keeping the aforementioned parameters constant, each type of vegetation formation (grassland, pine, pine–oak, open oak, or dense oak) was represented under three aspects (North, South, and East/West), with four replicates of each.

The selection of stands followed a systematic approach including geo-spatial mapping and a stratified random selection. Freely available advanced space-borne thermal emission and reflective radiometer (ASTER) digital elevation model (DEM) with 30 m spatial resolution was used to obtain topographical attributes like slope, aspect, and elevation. Slope and aspect were computed from the DEM using spatial analyst geoprocessing tool in ARC GIS 10.0. The geological map for the study area from Valdiya (1980) was scanned, geo-referenced and digitized to be used as a spatial layer in site selection. A land-cover map of study area showing all five vegetation formations of interest to the study was prepared through supervised classification of LANDSAT satellite imagery which was further refined based on the forest type map of Uttarakhand provided by the Forest Survey of India. A spatial overlay of all site characteristics (slope, aspect, elevation, vegetation formation, and geology) was performed using overlay tool in ARC GIS 10 to get a site-selection map. A 3 × 3 km sequentially numbered grid was overlaid on the site-selection map. Out of these, the sequence of grids for sampling was selected through a computer generated random number. Within each grid, all stands greater than 0.5 ha were listed, and one stand of each vegetation formation in each aspect type was again randomly selected. This procedure was followed until each vegetation formation was represented by four replicates in all three aspect categories. In addition, since forest fires have played an important role in driving the successional dynamics of the Himalayan forests (Brown et al. 2011; Joshi et al. 2013) they was specially assessed to evaluate the effect of fire on regeneration function of vegetation. According to Ashton et al. (2014) the most crucial component in promoting regeneration under pine canopy is protection from fire. Consequently a prolonged absence of fire, under a pine canopy, should lead to the regeneration of late-successional species in the presence of propagation units. To analyse this connection between the two successional stages based on fire occurrence, two fire categories (recent fire and old fire) were delineated based on fire scars and freshness of charring on tree trunks. We attempted to have both fire frequencies equally represented in the final sampled plots. However, there were no clearly identifiable recently burnt open or dense oak stands in the study area; in grasslands, fire signs could not be detected since the study was conducted post monsoon and the grass had regenerated removing all signs of past fire. Therefore, fire categories could only be justifiably assessed in pine and pine–oak mixed forests.

Data were recorded from 252 vegetation plots in total distributed over 84 stands (60 stands with old fire signs covering all vegetation formations and 12 stands each of pine and pine–oak stands with fresh fire signs). A pre-tested nested plot design with vertical stratification of vegetation based on height and diameter of species was used for data collection (Table 1). A

Table 1 Vegetation data collected in the nested plot

Vegetation strata	Plot size	Information collected
Tree seedlings (> 0–30 cm height)	1-m-radius circular plot	Species level data: species name, number of individuals, number of damaged individuals[b]
Tree saplings 1 (30–130 cm height)	3-m-radius circular plot	Species level data: species name, number of individuals, number of damaged individuals[b]
Tree saplings 2 (> 130 cm, < 3.18 cm DBH)	3-m-radius circular plot	Species level data: species name, number of individuals, number of damaged individuals[b]
Middle tree layer (> 130 cm height, ≥ 3.18 and < 7 cm DBH)	7-m-radius circular plot	Individual level data: species name, DBH, DRC, height, damage signs[a]
Canopy tree layer (DBH ≥ 7 cm)	10-m-radius circular plot	Individual level data: species name, DBH, DRC, height, damage signs[a]

DBH diameter at breast height 1.3 m above ground, *DRC* diameter at root collar 5 cm above ground, damages = grazing (G), burning (B), cutting (C), lopping (L)

[a] Presence of G, B, C, L recorded on individuals (y/n)

[b] Number of G, B, C, L individuals of a species recorded

transect starting at a distance of 20 m from the edge was laid at a 45° angle to the slope with the help of a compass. Data were recorded from three sampling plots on each transect, with a distance of 20 m between each plot.

Statistical analysis

What is the current state of successional development in the selected vegetation formations?

To understand the current state of successional development in the selected vegetation formations, the regeneration patterns and distributions of species were compared between stages. Functional traits of tree species can act as an efficient indicator of the successional stage of the vegetation community (Wilfahrt et al. 2014; Chai et al. 2015) and have often been used to understand and predict ecosystem function and the community structure and dynamics. The distribution of functional traits of tree species in the regeneration layers (i.e. tree seedlings and saplings) was used as an indicator to highlight the present successional regime in the study area. All tree species recorded during the survey were assigned to mutually exclusive categories of traits, based on available literature (Table 2). For each sampling plot, the number of individuals exhibiting early- and late-successional traits were used to estimate the per hectare distribution of individuals in each trait category. A non-metric multidimensional scaling (NMDS) ordination using Euclidean distance measure was performed to visualize the relationship between vegetation formations and functional traits of tree species in the regeneration strata.

In addition, vegetation structure and species composition across all vegetation strata were compared between the five vegetation formations. Structural characteristics across the five vegetation formations were compared on the basis of tree density for seedling, saplings, middle tree layer, and canopy trees. The density of trees was calculated based on the number of individuals and size of the plot. The mean values for tree density were compared using One-way Analysis of Variance. Followed by Games-Howell post hoc tests to determine the significance difference of among formations. Compositional difference across vegetation formations were compared through a multiple-response permutation procedure (MRPP) test in PC-Ord ver.6 (McCune et al. 2002).

How are anthropogenic disturbances affecting the growth, development, and succession in vegetation communities?

The impact of anthropogenic disturbances was analysed through disturbance signs on species and individual level recorded during the vegetation assessment. Information on disturbance signs was collected for grazing (includes browsing), burning

Table 2 Predominant traits of early- and late-successional species (Troup 1921; Champion and Seth 1968; Singh and Singh 1992; Gaur 1999)

Species trait	Complementary trait categories	
	Early-successional species	Late-successional species
Light demand	Light demanding in early years of development	Shade demanding in early years of development
Nutrient demand	Low (can grow on relatively infertile soils include rocks)	High
Water demand	Low	High (well drained soils)
Number of seeds	High	Low
Seed viability	High	Low
Dispersal	Wind	Animal assisted

(damage done by fire), cutting (complete removal of the above ground biomass of woody plants at the base of stem) and lopping (partial removal of biomass by deliberate cutting of branches from woody plants). This information was used to determine a disturbance (Grazing/burning/lopping/cutting) ratio for each vegetation strata on the following formula:

$$\text{Grazing/burning/lopping/cutting ratio} = \frac{\text{Number of grazed, burnt, lopped or cut individuals}}{\text{Total number of individuals}}.$$

The overall disturbance ratio at plot level was computed by taking a mean of disturbance ratios obtained from individual strata, for each disturbance. The mean disturbances ratios across vegetation formations were compared using one-way ANOVA, followed by post hoc tests to determine relative influence of disturbance regimes across vegetation formations.

The influence of grazing on the regeneration of late-successional oak was assessed through percentage grazing signs of oak individuals in each vegetation strata, across the five vegetation formations. Similarly, the percentage lopping of Oaks across vegetation formations in all vegetation strata was analysed to identify patterns of oak lopping at every stage of growth. The pattern of tree species regeneration in stands with early and fresh fire signs was also analysed and compared to identify the influence of fire occurrence on the successional regime in the study area.

Results

Current state of successional development

The distribution of functional traits of regenerating tree species reveals a significant overlap between the five vegetation formations. While early-successional traits (e.g. low nutrient demand and drought tolerance) are limited to grasslands, pine, and pine–oak forests, tree species with late-successional traits (e.g. high nutrient demand, high water demand, and shade tolerance) can be found regenerating in all vegetation formations except grasslands (Fig. 2).

The highest density of tree seedlings per hectare was found in grasslands and dense oak forests with no statistically significant difference between them (Fig. 3). Pine and open oak forests followed with second highest seedling densities which were significantly lower than grasslands and dense oak forests (Fig. 3). The lowest seedling density was seen in pine–oak mixed forests (Fig. 3). Data from tree sapling 1 and 2 strata were combined to get an overall trend of tree sapling regeneration across the five vegetation formations. Dense oak forests had the highest regeneration density. However grasslands, which had values for seedling layer density similar to dense oak, had the lowest density in this stratum (Fig. 3). Open oak, pine–oak, and pine forests had comparable values of sapling density across the five vegetation formations with no statistically significant differences between them. Middle tree layers also exhibit a similar trend where dense oak forests had significantly higher density of individuals per hectare than all vegetation formations, followed by open oak, pine–oak, and pine with comparable values. In the canopy tree layer,

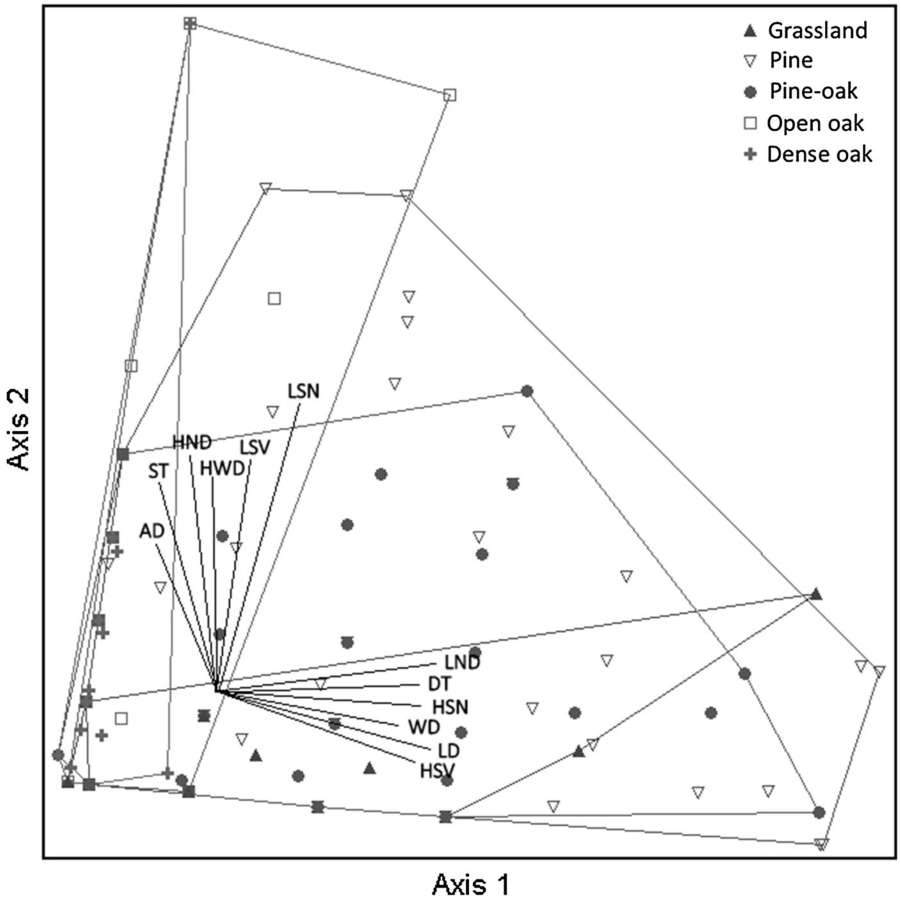

Fig. 2 Results of NMDS ordination examining species traits distribution in the tree regeneration layer. The composition dataset for both figures was based on species cover by plot (the ordination used Euclidean distance, was iterated for two dimensions). Symbols represent individual plots coded by vegetation formation (grassland, pine, pine–oak, open oak, and dense oak). Lines represent species trait distribution with in an increasing gradient where length of the line is proportional to the correlation between the variable and the ordination. *ST* shade tolerant, *LD* light demanding, *HWD* high water demand, *DT* drought tolerant (or low water demand), *HND* high nutrient demand, *LN* low nutrient demand, *WD* wind dispersed, *AD* animal dispersed, *HSN* high seed number, *LSN* low seed number, *HSV* high seed viability, *LSV* low seed viability

density per hectare was significantly higher in dense and open oak forests compared to pine–oak and pine forests. Grasslands had a very small value in this category, as expected (Fig. 3).

We found significant compositional differences among the five vegetation formations across all vegetation strata with statistically significant negative T values from the MRPP test (Table 3). The within-group agreement statistic (A statistic) for all vegetation strata shows a fairly low values ($A < 0.3$), except for the canopy tree layer, indicating low within-group homogeneity (Table 3). However, according to McCune et al. (2002), A statistic values are usually less than 0.1 in community ecology, which is in concordance with our results.

Effect of anthropogenic disturbances on growth, development, and succession in vegetation communities

The disturbance regime had a strong impact on the vegetation and regeneration of all associations. A comparison of disturbance (grazing, burning, cutting, and lopping) ratios between vegetation formations revealed that grazing was almost equally present in grasslands, pine, pine–oak, and open oak forests while dense oak forests had relatively less grazing pressure

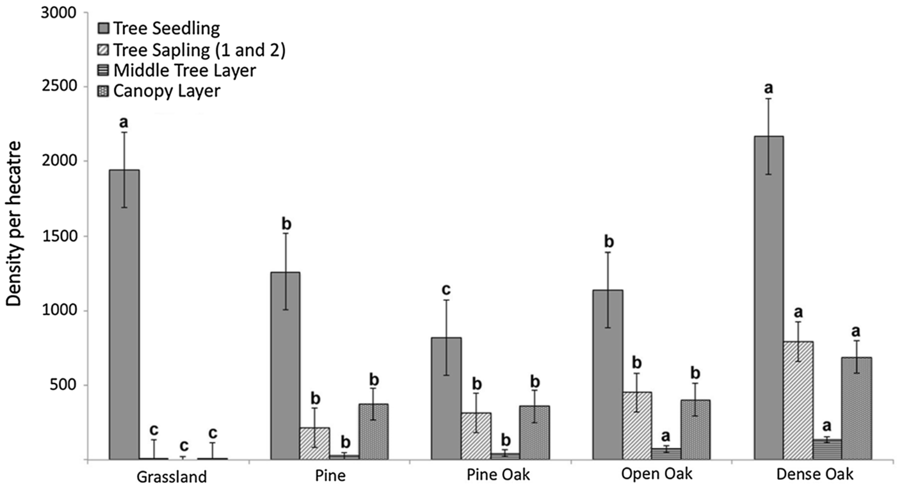

Fig. 3 The mean tree density per hectare of tree seedling layer (> 0–30 cm height), sapling (sapling 1: 30 to < 130 cm height and sapling 2: > 130 cm, < 3.18 cm DBH), middle (> 130 cm height, ≥ 3.18 and < 7 cm DBH), and canopy layers (DBH ≥ 7 cm) across the five vegetation formations representing a theoretical successional sequence. The letters (*a*, *b*, *c*, *d*) qualitatively indicate significant differences (*a* > *b* > *c* > *d*) according to Games-Howell post hoc test, differences reported as significant where $p < 0.05$

Table 3 Multiple-response permutation procedure (MRPP) analysis to compare species compositions between all vegetation strata of grasslands, pine, pine–oak, open oak, and dense oak forests

Vegetation strata	*T* statistic	*A* statistic	*p* value
Tree seedlings (< 30 cm ht.)	− 21.01	0.19	0.000
Tree saplings 1 (> 30–130 cm ht.)	− 4.37	0.05	0.0003
Tree saplings 2 (> 130 cm ht., < 3.18 cm dbh)	− 4.06	0.04	0.0009
Middle tree layer (> 130 cm ht., < 7 cm dbh)	− 10.5	0.05	0.000
Canopy tree layer (> 7 cm dbh)	− 55.6	0.04	0.000

Dbh diameter at 1.3 m, *Ht* height

(Fig. 4). Burning was highest in pine and pine–oak forests, with barely any fire signs in the other vegetation formations. Lopping was highest in open oak forests (Fig. 4). Cutting was not as widespread as the other forms of disturbance and was mainly seen only in forests with oak species.

The effect of grazing on tree regeneration was clearly visible in all vegetation formations, especially on oak species. Oak species regenerated abundantly in all vegetation formations; however, most of the individuals were found grazed. The percentage of regenerating oak individuals with grazing signs was greater than 50% across all vegetation formations (Fig. 5). The total number of oak individuals regenerating per hectare declined from seedling to sapling stage, with dense oak forests showing the highest survival (Fig. 5). High grazing pressure on oak species often forced them to occur in a bush/mat-like formation.

In addition to grazing, forest fires are known to influence the vegetation in the study area (Joshi et al. 2013; Kumar et al. 2013). The distribution of species in the seedling layer (< 30 cm) in pine and pine–oak stands with fresh and old fire signs showed a preponderance of pine regeneration in both fresh and old burnt stands of pine and pine–oak forests (Fig. 6). However, in stands with old fire, the proportion of oak regeneration was significantly higher than that in stands with evidence of recent fire. Similarly, in the sapling1 regeneration strata, stands with fresh fire signs in pine forests show much higher number of pine saplings compared to other species like *Q.*

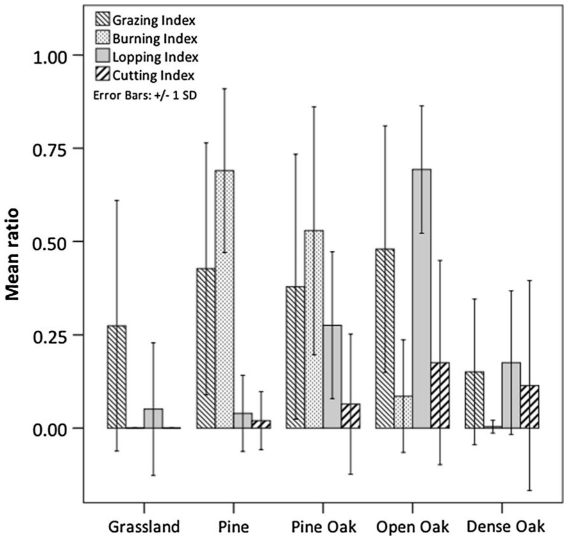

Fig. 4 Comparison of mean grazing, burning, lopping, and cutting ratios/index in grasslands, pine, pine–oak, open oak, and dense oak vegetation formations, across all vegetation strata

leucotrichophora, *Q. floribunda, Litsea umbrosa*, and *Ficus roxburghii* (Fig. 6). Stands with old fire stands, however, had a clear majority of oak species. Saplings in pine–oak mixed forest stands with recent fire had relatively equal proportions of pine and oak species; however, in stands with old fire, the number of individuals per hectare was higher for oak species.

Sapling 2 vegetation strata in pine forests with recent fire mainly had pine species with few individuals of *Rhododendron arboreum* and *Litsea umbrosa* whereas the stands with older fire show a much larger number of oak individuals along with pine. Similarly, pine–oak forests with recent fire had a much greater proportion of pine than sites with older fire signs (Fig. 6).

Lopping primarily affected oak trees in the middle and canopy layer. Pine-oak forests had the highest rate of lopping (62%) in the middle tree layer followed by open oak (55%), and dense oak forests (25%) (Fig. 7). In the canopy tree layer, open oak forests, which were a result of chronic lopping in dense oak forests, exhibit the highest level of lopping with 81% of the total trees in a hectare showing signs of damage. High lopping damage in open oak forests was followed by pine–oak mixed forest and dense oak forests, with 42 and 31% of the total trees exhibiting lopping signs in a hectare of forestland, respectively (Fig. 7). Out of the limited number of trees found in grasslands, 43% had lopping signs.

Discussion

Our results indicate that even though there is a potential of a progressive succession from grassland and pine forest towards an oak forest community, chronic disturbances limit the growth and development of regenerating seedlings and saplings. This

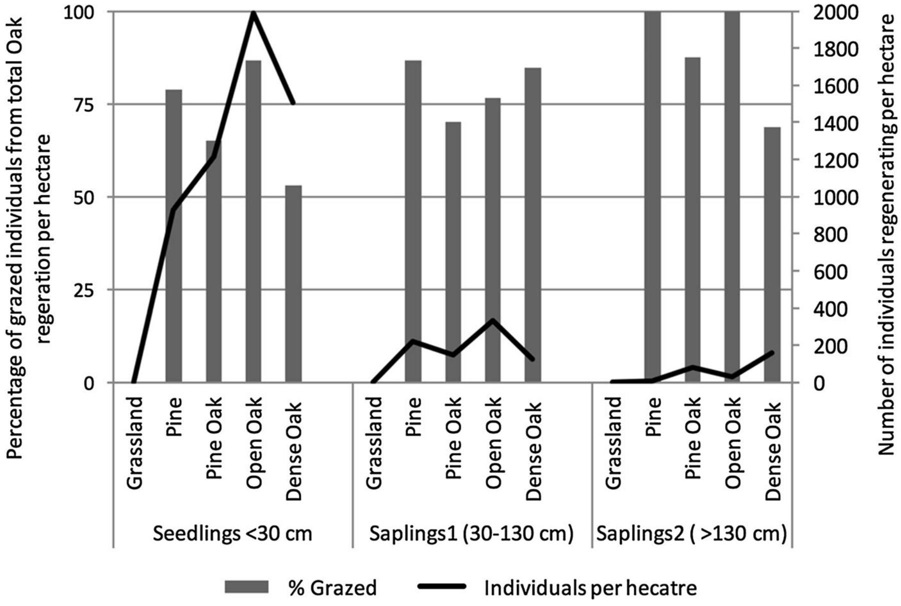

Fig. 5 Total regeneration of oak per hectare and percentage of grazed individuals in seedling (> 0–30 cm height), sapling (sapling 1: 30 to < 130 cm height and sapling 2: > 130 cm, < 3.18 cm DBH), strata of regeneration

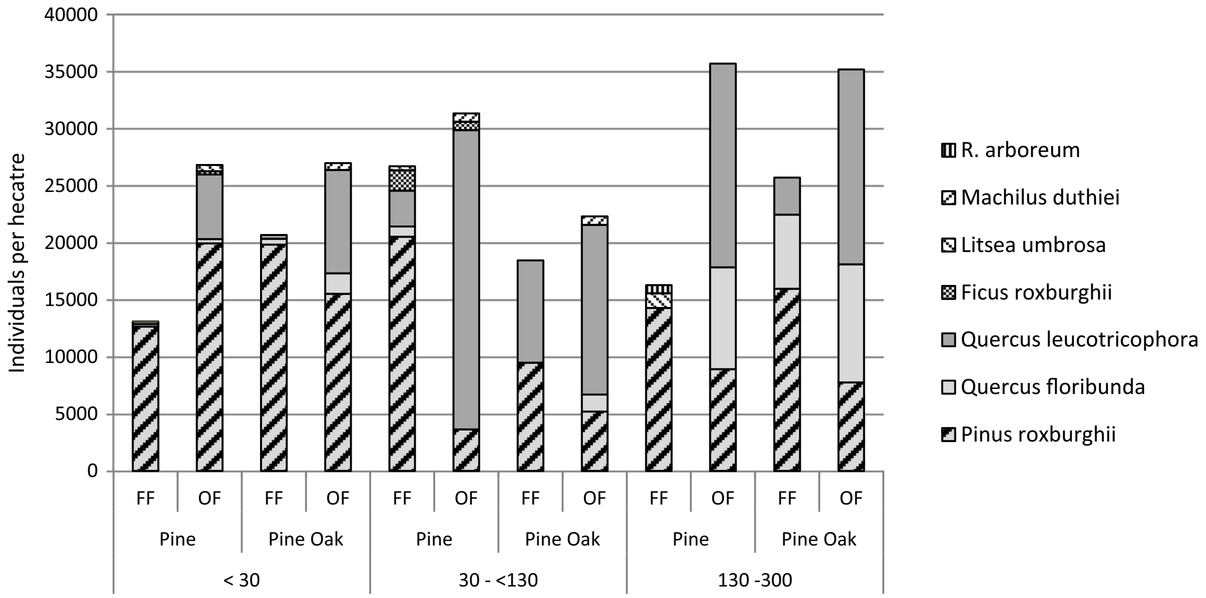

Fig. 6 Distribution of species in pine and pine–oak stands with fresh fire (FF) and old fire (OF) signs in tree seedling layer (> 0–30 cm height), sapling 1 (30 to < 130 cm height), and sapling 2 (> 130 cm height and < 3.18 cm DBH)

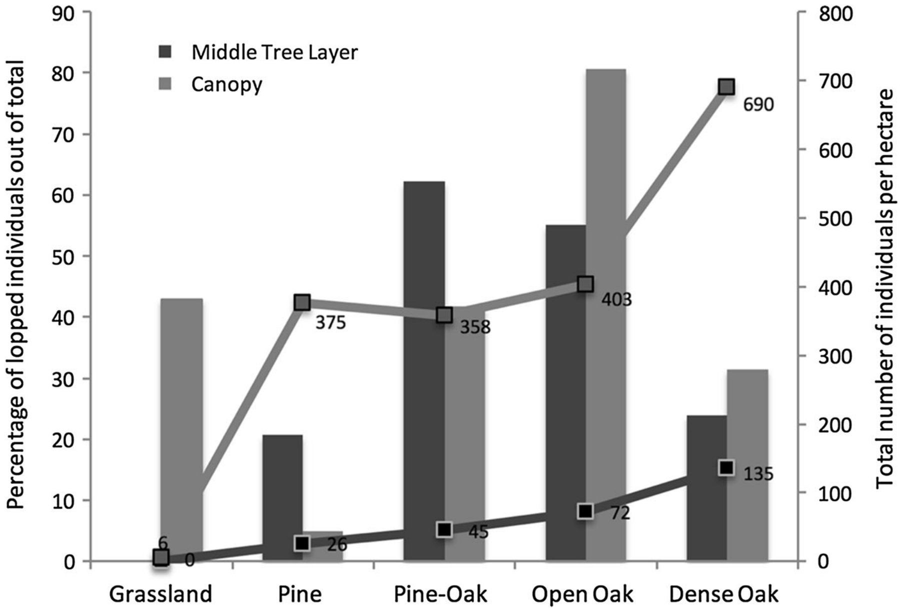

Fig. 7 Percentage Lopping signs on middle (> 130 cm height, ≥ 3.18 and < 7 cm DBH) and canopy layer (DBH ≥ 7 cm) trees in grasslands, pine, pine–oak, open oak, and dense oak vegetation formations

continued disturbance maintains the vegetation in an arrested phase of vegetation succession.

The distribution of functional traits of tree species regenerating across the five vegetation formations represents a progressive successional trend with species possessing late-successional traits (e.g. *Quercus leucotrichophora, Q. floribunda,* and *Rhododendron arboreum*) regenerating in early-successional pine and mid-successional pine–oak forests. In terms of structural attributes of the vegetation communities, a striking observation is the statistical similarity in tree regeneration density between early-successional grasslands and late-successional dense oak forests, both showing profuse regeneration of tree seedlings (Fig. 3). However, the compositions of species regenerating in the two vegetation formations are entirely different (Table 3). Grasslands harbour primarily light-demanding, early-successional *Pinus roxburghii* species, while oak forests, on the other hand, foster the regeneration of *Quercus leucotrichophora* along with *Rhododendron arboreum, Cornus macrophylla*, and *Myrica esculenta*. In the advanced phases of the regeneration layers (i.e. tree sapling), the compositional variation among vegetation types is considerably lower than that for tree seedlings (Table 3).

Such trends in species distribution in the regeneration strata are a positive sign for the potential development of early- and mid-successional forests into later-successional communities in the future. However, we find that a progressive successional transition towards a late-successional broadleaved oak forest community has been restricted by disturbances. This chronic disturbance regime results from the intensive interaction between people and forests to extract ecosystem products for maintaining local livelihoods (Kumar and Ram 2005; Makino 2011; Singh et al. 2014). Such resource-extraction methods (or anthropogenic disturbances) change the structure and composition of the forest by altering tree biomass and diversity (Onaindia et al. 2004; Bongers et al. 2009). In this study, the main anthropogenic disturbances identified include grazing, burning, lopping, and cutting (Fig. 4).

More than 50% of regenerating oaks were grazed across all regeneration strata (Fig. 5), inhibiting their establishment and development into mature trees by converting them into a multi-branched, shrubby form instead. The extreme reduction in the number of stems that successfully transition from seedling-to-sapling stages highlights the low survival percentage of germinated seedlings (Fig. 5). Even though gradual thinning of density from seedling-to-sapling stages is a natural phenomenon, intensive grazing pressure in the study area augments this process leading to high seedling mortality (Thadani and Ashton 1995; Seiwa 2007). Although grazing has been extensively studied, there is no clear consensus on the effect of grazing on forest ecosystems in the Himalayas (Roder et al. 2002; Buffum et al. 2009). While some studies claim that grazing is necessary to maintain species diversity (Negi et al. 1993; Austrheim and Eriksson 2001; Noor Alhamad 2006), there are other studies that show a negative influence of grazing on diversity, biomass, abundance of palatable species, and the rate of increase in tree cover (Hernández and Silva-Pando 1996; Carmel and Kadmon 1999; Ford et al. 2012). However, according to Olff and Ritchie (1998), grazing can have either a negative or positive effect on species diversity and richness depending on the abundance of herbivores. Current grazing pressure in most vegetation formations of Central Himalaya is with an average cattle density of 7.9 individuals/ha (Samal et al. 2003), much higher than levels that would allow the establishment of palatable broadleaved tree species such as oak. Buffum et al. (2009) showed that moderate intensity of grazing, with cattle abundance of 0.4 cattle/ha or less, in broadleaved oak forests, did not significantly change forest ecosystem productivity, highlighting the potential to maintain sustainable grazing in these landscapes.

In addition to grazing, early-successional vegetation types are also severely affected by recurrent forest fire, which acts as a central driver of vegetation dynamics. Most forest fires in the region are anthropogenic in nature, deliberately set in order to increase grass cover and forest accessibility, or are accidental outbreaks from burning of agricultural fields, solid waste burning, and careless smoking (Joshi et al. 2013; Kumar et al. 2013). Fire events are supported by the accumulation of highly flammable needles in the pine forest understory (Brown et al. 2011; Joshi and Tewari 2011). Incidentally the needle fall season (May–June) coincides with peak fire season during the hottest months of the year, which is the peak fire season, subsequently escalating the intensity of damage (Chandran et al. 2011). Chronic fires reduce soil organic matter, soil nutrients, moisture, and trigger erosion (Shakesby 2011; Kumar et al. 2013) effectively creating conditions suitable for establishment of early-successional species (Semwal and Mehta 1996; Retana et al. 2002; Nyamai et al. 2014). Frequent fires also remove the litter layer from forests which reduces the establishment of large seeded species (like oak) by drying seeds and soil (Seiwa 2007). High fire frequency in grasslands also inhibits the establishment of pine seedlings since they are vulnerable to fire when young. However, regular fires clearly hinder the establishment of late-successional tree species which are in general fire sensitive (see Ashton et al. 2014). If fires are absent for a longer time period, we find a relative increase in the density of late-successional oak species in pine and pine–oak forests (Fig. 6).

The regeneration of oak in pine understories, as recorded in this study, is contrary to the perception that oak seedlings cannot establish under pine (Sinha 2002). The ability of pine to support the growth of native and late-successional species in the absence of disturbance has been established by past studies (e.g. see Onaindia and Mitxelena 2009; Ashton et al. 2014). Therefore, protection of pine stands from fire along with the assisted regeneration of oak under pine forest canopies can be utilized as a management tool to push the successional dynamic towards broadleaved oak forests in the study area. However, to ensure successful regeneration and development of late-successional oak species under pine canopies, reduction of grazing pressure is equally important.

The direct influence of burning and grazing was found to be comparatively low in mid- and late-successional vegetation, where lopping is the most intensive disturbance. Two of the most significant livelihood resources, i.e. fuelwood and fodder, have been traditionally procured via lopping of oak trees (Makino 2011). Lopping directly affects the standing tree biomass, through small-scale removal of branches. Out of the total oak trees in the canopy layer of an open oak forest, 81% showed lopping damage in the landscape (Fig. 7). Since productivity and other ecosystem processes are directly related to above ground biomass (Lohbeck et al. 2014) a decrease in biomass compromises the productivity of oak forests. Analysis of competitive dynamics of oak seedlings in the Himalayan forests by Thadani (1999) revealed that chronic lopping which increases light availability on ground to create open oak forests has fostered the replacement of oak with early-successional pine forests. The dehydration and loss in viability of oak acorns in lopped forests gives a direct competitive advantage to pine, a light-demanding pioneer specie. The chemical, physical, and hydrological properties of forest soil are also influenced by lopping, due to reductions in litter which lowers soil nutrient concentrations, further reducing the establishment of nutrient demanding late-successional species (Thadani and Ashton 1995; Singh and Rawat 2012; Singh et al. 2014).

The plant community reacts to the intensity and frequency of disturbances through the preferential regeneration of species better adapted for the available site conditions. Over time, the continued differential regeneration of species determines the vegetation structure and composition in a forest stand. While high disturbance pressure selects for early-successional species such as pine, a reduction in disturbance intensity has been found to be beneficial for the growth and regeneration of late-successional species in the central Himalayan forests. Such disturbance-driven dynamics also give rise to variation in phytosociological attributes of vegetation, including species diversity, composition, and structure, which govern overall ecosystem functioning and ecosystem service supply (Royo and Carson 2006; Lasky et al. 2014; Whitfeld et al. 2014).

Conclusion

Our results highlight that site conditions across the landscape do not limit successional dynamics, and therefore the potential supply of ecosystem services. Early-successional vegetation communities in the study area have the potential to resume successional development out of their present arrested successional stages, in the absence of anthropogenic disturbances.

While late-successional oak forests are best suited to support livelihood needs of the local people (Joshi and Negi 2011; Naudiyal and Schmerbeck 2017), their regeneration and development in the study were found to be severely threatened by chronic disturbances in both early- and late-successional vegetation which maintains early-successional vegetation in an arrested stage. Therefore, the presence of an early-successional stage, due to chronic anthropogenic disturbances, indicates a suboptimal management approach, with gross underutilization of forest productivity and the provision of ecosystem services.

In a scenario where forests are managed from ecosystem services supply, assisted manipulation of forest structure and composition through silvicultural techniques accompanied by controlled disturbances in preselected areas with early-successional vegetation formations, such as pine forests, can effectively foster the regeneration of late-successional species in its understorey.

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