Plant species diversity in unmanaged moist deciduous forest of Northern India

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The present study examines species recovery and change in community composition four decades after the management plan completely constrained all silvicultural activities in Doon Valley (India) moist deciduous sal forests (*Shorea robusta*). These forests experienced intensive commercial logging for an extended period (> 100 years). To discontinue disintegration and improve the diversity and regeneration, these were declared protective and consequently all silvicultural activities were abandoned. For this, species richness and regeneration were studied in the context of overstorey structure, employing nested quadrat method. Out of 130 species reported in the earliest-most study from these forests, only 68 species were recorded here. Change in community composition has taken place with *Mallotus philippensis* becoming dominant in one community; this association is new for these forests. Effect of overstorey structure was noticeable, highest species richness and diversity were increasing with a decrease in tree density and basal area. These forests showed impaired regeneration progression; for all the groups there was a wide gap between the seedlings and saplings conversion to advance stages. Prospects of recovery are fair as several tree species were reported in juvenile stages with adequate density. Results demonstrated that conversion of forests having a long history of exploitation to protected forest is initially good, but for successful recovery, after a restitution time, it is desirable to emulate intermediate disturbance by selective harvesting of old and malformed trees. This will initiate gap-phase regeneration and channelize resources to lower diameter class trees to develop.

Keywords: Diversity, overstorey, protected forest, regeneration, *Shorea robusta*.

THE composition and structure of forests are important attributes that manifest their health and underpin their diversity[1]. The perpetuity of services accruing from forests is intricately tied to their health, which effectively depends on the choice of forest management strategies. Therefore, understanding the effect of forest management, both past and present, becomes a key focus in maintaining biodiversity in forest ecosystems[1–4].

Various silvicultural treatments integrated into a forest management plan affect diversity and ecosystem processes differently. The results obtained from studies show that tree harvesting (a disturbance event *sensu* Roberts and Gilliam[1]), retention and conservation-stated zero structural manipulations influence the diversity, regeneration and recruitment of both overstorey and understorey species[5–7] and younger diameter class tree species density[8], both positively[9] and negatively[10], depending upon the intensity and magnitude[3,9]. It is emphasized that effectiveness of conservation efforts entails garnering comprehensive knowledge of forest management strategy effects on species diversity, their abundance and dispersion within an area of interest, as an important aspect of sustainable ecological management, because it promotes understanding about the relationship between strategies and species composition[1,2]. These are more important for (sub-)tropical regions where the forest caters to two highly juxtaposed needs – one, wood supply and second, they are the largest repositories of global biodiversity.

Among deciduous forests, *Shorea robusta* Gaertn. F. (sal) forests are important habitats and account for ~ 12% of the total forest cover in India. Within sal belt of the Himalayan foothills, Doon Valley secondary coppice sal forest primarily represents moist habitat. These forests were indiscriminately harvested over an extended period of time (> 100 years) under feudal governments and later under colonial rule. Since the start of scientific management under colonial rule (1860) until abandonment of silvicultural activities these forest were worked under several management systems, all with timber-centric approach, and as a management practice miscellaneous inferior (non-)timber species were selectively removed and their regeneration was curbed. Consequently, to discontinue degradation and minimize the negative impacts that indiscriminate harvesting had inflicted upon these forests, latter-day management plans notified them as protective forest. Thereafter, all activities responsible for the deconstruction of plant diversity ceased four decades back. The fundamental shift in management goal from production to conservation forestry was introduced to

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integrate efforts to reinstate and thereafter increase the diversity and long-term health of the forest by excluding the harvesting and related disturbances. Assertion behind the perspective was that with no interference, forests would be exposed only to natural disturbance regimes. Following this, multi-tier structure will develop and subsequently lead to gap closing, increase in structural diversity, appearance of some late successional species and diverse microsite conditions with a potential to augment diverse understorey growth.

As a management strategy, closing a forest to exclude all silvicultural activities so as to mimic only natural disturbance effects is not a new ecosystem management tool in tropical forests[11]. As an important conservation strategy, forests are designated protected when it is recognized that the need for conserving plant diversity for their ecological restoration outweighs untenable timber extraction. Adoption of this has become more common and is being applied to a larger scale now[12,13]. Compared to the increasing number of studies conducted on gauging the effects of forest management decision about overstorey manipulation on the understories[3–5,7,9] and regeneration[14,15], relatively few studies focused on overstorey structure and composition effects on understorey and regeneration following no intervention decision where management plan declared as a protective forest[6]. However, a need was felt that they should be complemented with other management strategies, especially harvesting, as a part of one comprehensive management strategy, not just to maintain but increase diversity, regeneration and dispersal[2,16]. At the same time, it is equally important to understand the response of these alternative management strategies on both overstorey and understorey plant species because any change in management strategies can affect the compositional and structural development of the forests. One of the main effects of harvesting is that removal of old and mature trees alters the age-class distribution, by increasing the abundance and distribution of younger classes[3,8]. It is therefore important to understand the ways in which retention of mature trees influences the species diversity.

From here onwards management strategies for such forests could involve: (a) continuance of no artificial intervention to increase diversity and evenness, (b) altering structure so as to emulate multicohort structures – as mosaic of different ages and developmental stages and diversify the microclimatological conditions for successful colonization and dispersal of natives and/or (c) selectively removing overmature trees with perpetual timber supply without jeopardizing the multiple benefits from them. Depending on the characteristics of the management, i.e. its spatio-temporal spread and magnitude, the forest may show a response varying from resistance, via recovery with more or less complete return to the initial state[16]. However, there is a lack of knowledge of the length and continuance of restitution time of abandonment of harvesting on recovery of the characteristic species diversity and composition in the tropical region. And it is particularly relevant for forests which are dependent on natural regeneration to maintain their overstorey structure, particularly that of umbrella species, and through its effects, on understorey vegetation structure too. Therefore, the main aim of this study is to describe the extent of recovery of the species diversity and composition after 40 years following abandonment of silvicultural activities and other management applications, except manual clearing of the fire lines following summer. However, like many other tropical forests elsewhere, long-term past records of species diversity composition and structure are not available for these forests for comparison, except the study by Seth and Bhatnagar[17], covering limited scope. We started our study on the premise that species richness must have increased in these forests following the withdrawal of interventions. Divergent to this is the view that fairly long protection cannot by itself return a forest to species-rich state (or initial state) even after stopping all the silviculture operations and removing associated disturbances. Here we have described the structure and composition of overstorey and understorey in order to evaluate the protection related no manipulation in overstorey effect on species richness, diversity and regeneration. Results of the study could facilitate recommendations about management of forests which are abandoned or declared protected.

Material and methods

Study site

Field survey was conducted in the Doon Valley (area ~ 3008 km^2; 29°55′ and 30°30′N; 77°35′–78°24′E; 600–800 m amsl; see Supplementary Information, Figure S1, online). Climate of the area is tropical; where average maximum and minimum temperatures are 27.65°C and 13.8°C respectively, and average annual rainfall is 202.54 cm. The soils are developed on the deep alluvial deposits with parent material derived from the Doon alluvium.

About 52% (1607 km^2) of the Doon Valley encompasses subtropical deciduous forests, with high abundance of sal (> 80%), sometimes forming pure crop over extensive areas. In these subtropical moist deciduous forests, sal is the dominant overstorey species with *Mallotus philippensis* as co-dominant tree and *Clerodendron viscosum* as understorey associate species. All the past studies clearly distinguished four different layers in these forests with sal and *Terminalia alata* occupying the top storey followed by *Syzygium cumuni* in the middle storey and *M. philippensis* and *Ehertia laevis* in lowermost tree canopy and understorey shrub and herb layer. Conservation of these forests was started when the East and West Dehradun Forest Divisions were reorganized in 1986 into a single Dehradun Forest Division.

Field survey

Phytosociological studies were conducted using nested quadrat method during 2007–08. Quadrats were laid along a transect line with a gap of 20 m between the two quadrats. A total of 75 quadrats (25 at each site), each of 100, 9 and 1 m^2 size were laid to inventory tree, shrub and herb layers, respectively[18]. In each quadrat, the number of individuals for abundance and diameter of each species was recorded. Number of individuals was analysed for relative values of frequency, density and basal area (BA), and finally importance value index (IVI) of each species was computed by summation[18]. Plants were assigned to different layers based on the height – tree layer, including woody species with > 5 cm diameter; shrub layer, including woody species having > 1 m height and 1.5–5 cm diameter, and herb layer, including all species < 1 m height. Trees saplings and climbers were enumerated with shrub layer, and tree and shrub seedlings with herb layer. The number of species recorded represented species richness and further floristics was described by Shannon–Wiener index (H'), Simpson's index (Cd), Evenness (J') and Jaccard's similarity coefficient (C_J)[19]. Tree species regeneration was studied using the relationship between density of seedlings, saplings and mature trees. Three categories – stable/balance, gap colonizers and poor were identified. The regeneration was stable/balance when a good number of seedlings/saplings and mature trees (> 10 trees/100 m^2) were present; gap colonizers when a good number of seedlings/saplings along with mature (< 10 trees/100 m^2) were present, and poor when seedlings/saplings density was less than that of mature trees.

Soils collected (20 cm) from all the plots were dried and sieved (2 mm). pH was determined in 1 : 2 soil–water suspension using glass electrode pH meter (Systronics 335). Soil moisture was estimated with moisture analyser (Sartorius MA 50). Soil temperature was recorded at the time of sampling in every plot.

Data analysis

Multivariate hierarchical cluster analysis using agglomerative hierarchical cluster (AHC) techniques was used to define communities. Sørenson (Bray–Curtis) dissimilarity (distance measure) and flexible β (–0.25; fusion strategy) were used to determine communities relatedness[20]. Species present in < 5% of plots were eliminated from the analysis. In PC-ORD, prior to analysis, outlier analysis based on the cut-off point of 2σ from mean abundance recognized nine plots as outliers and hence removed them from the final analysis. Indicator species analysis was then used to assign species that are indicative of a particular group of sites based on the indicator values generated. Statistical significance ($P < 0.05$) of species indicator values in each group was tested using Monte–Carlo tests with 1000 randomizations[21]. Significant difference between the groups for various variables was tested with ANOVA using XLStat (Addinsoft, NY).

The interrelationship between plant communities was analysed using non-metric multidimensional scaling (NMDS). The PC-ORD-4 package was used for the cluster analysis and NMDS. The degree to which the floristics patterns are environment-driven was explored with canonical correspondence analysis (CCA). CCA was performed on CANOCO v4.5 using Monte-Carlo permutation technique with 1000 permutations under restricted model[22]. Earlier studies underlined the defining effect of soil moisture, temperature and pH in species distribution in these forests along with the stand composition and structure effects[23]. Hence, soil moisture, temperature and pH and basal areas of important sal associate trees were used to understand their effect on assemblages within a community.

Results

General species composition

A total of 68 plant species (63 genera, 42 families) were recorded. Most of the species enumerated in the survey were toward rarity (Table 1). Among trees, middle layer was relatively rich (7 species) compared to the top canopy (4 species). Shrubs and herbs together accounted for ≈ 90% of inventoried species (see Supplementary Information, Table S1, online). There were 28 species in sapling and seedling stages (23 tree saplings, 4 tree seedlings and 4 shrub seedlings). However, as many as 13 tree species saplings encountered were not represented as subsequent growth stages (see Supplementary Information, Table S1, online).

Table 1. Number of rare species recorded in different groups from sal forest

		No. of rare species[a]		
	Total species	GI	GII	GIII
Trees	11	8	4	6
Saplings	24	16	15	14
Seedlings	3	2	1	1
Shrubs	23	16	9	5
Seedlings	5	3	3	1
Climbers	4	3	2	1
Seedlings	5	5	2	3
Forbs	11	8	8	7
Grasses	2	1	–	1
Sedge	1	–	–	–
Ferns	2	2	1	–

[a] Rare species are present in < 20% of total plots.

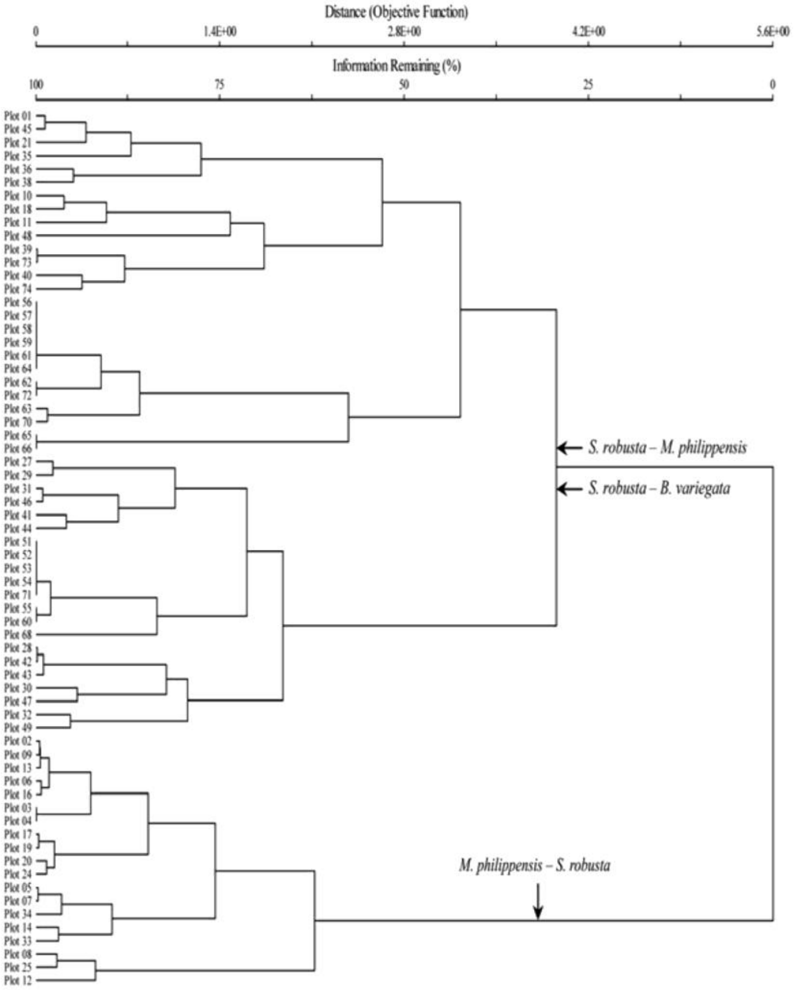

Figure 1. Dendrogram showing the different associations identified by the agglomerative hierarchical cluster analysis (AHC).

Agglomerative hierarchical cluster classification, species composition and diversity

Three groups, i.e. *S. robusta*–*M. philippensis* (G1), *S. robusta*–*Bauhinia variegata* (G2) and *M. philippensis*–*S. robusta* (G3) were classified (Figure 1; Table 2). From GI, 9 tree species were recorded and the group had density of 404 trees/ha. *S. robusta* (sal hereafter) and *M. philippensis* (*Mallotus* hereafter) were the most dominant species (Figure 2; see Supplementary Information, Table S1, online). High number of shrubs and saplings in the understorey and herbs and seedlings in the herbaceous layers was also recorded (Table 1; see Supplementary Information, Table S1, online). GII had 8 tree species with 710 trees/ha density. Sal with highest IVI and density was the most dominating species. In GIII, 9 tree species with high density (1029 trees/ha) were recorded. *Mallotus* (724 trees/ha) was the predominant species of this group (Figure 2). Shrub (and saplings) and herb (and seedlings) layers were arranged according to classified communities (see Supplementary Information, Table S1, online).

All diversity measures, except *Cd* were relatively higher for GI (Table 3 and Figure 3). *H*′ ranged between 1.05 (GIII) and 1.37 (GI) for trees, 2.61 (GIII) and 2.89 (GI) for shrub layers, and 2.58 (GII) and 2.89 (GIII) for herb layers. Tree and shrub layers of GIII were the most homogeneous and herb layers for GI and GII. Simpson's index varied between 0.08 (GII, shrub layer) and 0.53 (GIII, tree layer). Categorization of species into life-forms among various groups is shown in Figure 4. GIII was least diverse with minimum number of species for all the life-forms, except forbs (see Supplementary Information, Table S1, online).

Regeneration trends of the top three dominant species showed that sal regeneration was stable in GI (Figure 5). But very few individuals (< 5/100 m^2) of trees show enough gap for *Mallotus* to colonize successfully. Although *S. cumini* (hereafter *Syzygium*) was the third dominant species of the group, its regeneration was poor. In GII, sal had stable regeneration, *B. variegata* (hereafter *Bauhinia*) poor and *Mallotus* gap-colonizing regeneration trend. Unlike GI and GII,

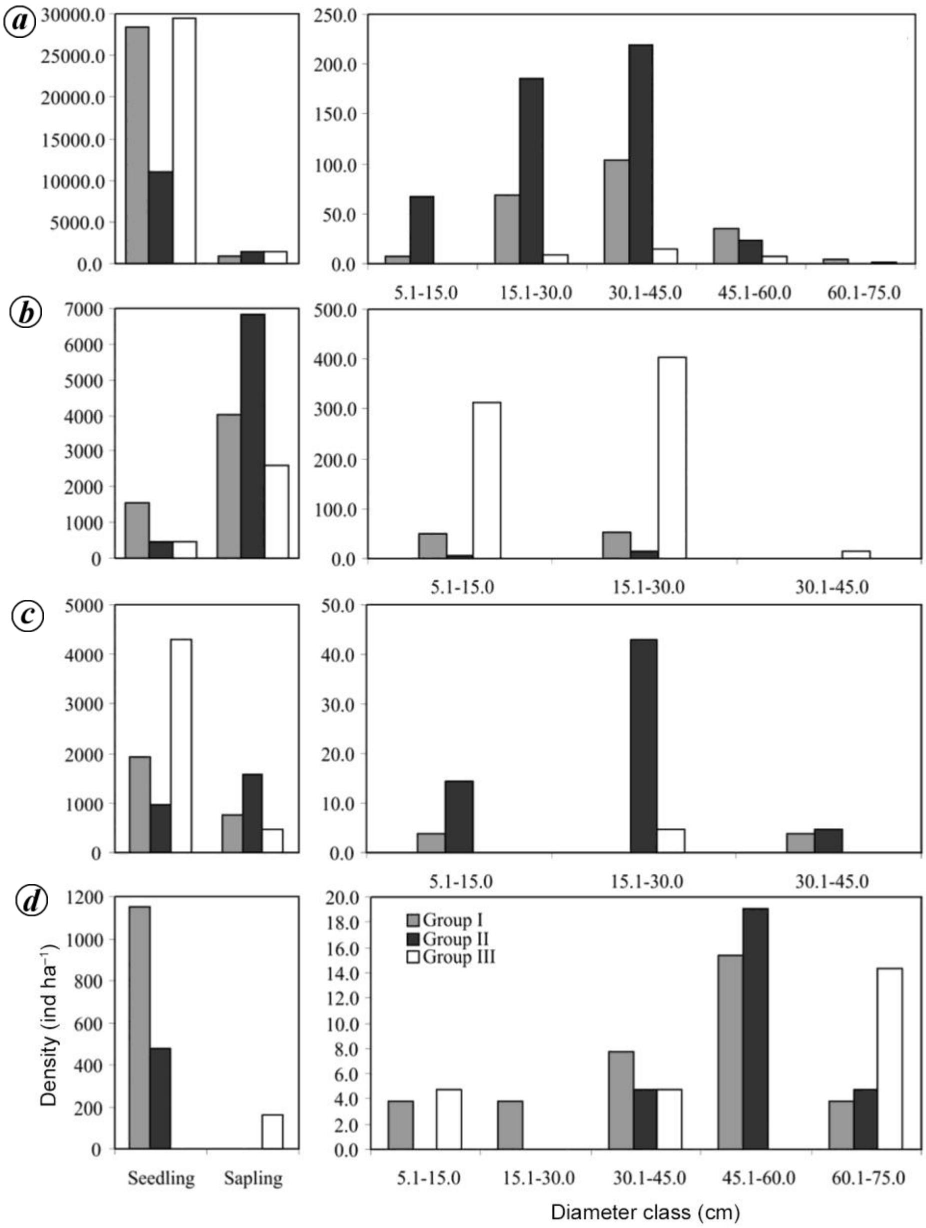

Figure 2. Diameter density classification of (***a***) *Shorea robusta*, (***b***) *Mallotus philippensis*, (***c***) *Syzygium cumini* and (***d***) *Terminalia alata* among different groups.

Mallotus population was stable and *T. alata* (hereafter *Terminalia*) poor in regeneration in GIII. Although maximum sal seedlings (259,048 seedlings/ha) were found in GIII, conversion to saplings was highest in GII (46.55%). The number of seedlings was disproportionately higher compared to mature population. Conversion of saplings to subsequent mature population was poor varying between 0.31 (GIII) and 0.96% (GII). The Pearson's correlation between density of seedling and sapling was negative ($r = 0.67$, $P < 0.002$), between seedling and mature crop negative ($r = 0.99$, $P < 0.0001$), and between sapling and mature crop positive ($r = 0.77$, $P < 0.0004$).

Relationship between tree species and communities with environmental variables

NMDS (see Supplementary Information, Figure S2, online) axis 1 separated GI from the other two groups. GIII was distinguished from the other two groups on axis 2. However, GI and GII had some affinities. CCA presented a strong correlation between environmental variables used in the analysis with vegetation. The Monte-Carlo test on the first canonical axis and all canonical axes with f values of 6.5 and 3.9 were significant ($P < 0.005$). The first two canonical axes cumulatively explained 90.7% (58.3% and 32.4%) of the total variance of species–environment

Table 2. Characteristics of soil and of various communities in moist deciduous forests of Doon Valley, India

Feature	GI	GII	GIII	*P*
No. of plots	26	21	19	
Soil temperature (°C)[a]	28.2 (3.8)	29.4 (0.9)	22.3 (2.5)	0.007
Soil pH[a]	6.2 (0.4)	5.8 (0.7)	6.0 (0.4)	< 0.0001
Soil moisture (%)[a]	8.9 (2.0)	9.5 (2.1)	10.1 (1.8)	0.001
Tree layer				
No. of species	9	7	9	0.004
Total density (trees/ha)	404	710	1029	0.04
Total basal area (BA; m^2/ha)	15.5	24.5	28.6	0.014
Density (trees/ha) – sal	219	505	157	0.01
BA (m^2/ha) – sal	10.8	19.9	12.6	0.02
Shrub layer				
No. of species[b]	45 (21)	42 (20)	31 (17)	0.01
Density (plants/ha)	52350	52751	50741	< 0.0001
Herb layer				
No. of species[c]	28 (10)	21 (09)	25 (09)	0.007
Density (plants/ha)	255000	113333	259048	0.04
Unique species	4	3	2	

[a]Values in parenthesis are standard deviations; [b]Trees saplings number; [c]Trees seedlings number and shrubs.

Table 3. Jaccard's index of similarity between different groups identified through cluster analysis

	Group	GI	GII
Tree	GII	0.60	
	GIII	0.64	0.45
Shrub	GII	0.79	
	GIII	0.60	0.58
Herb	GII	0.69	
	GIII	0.89	0.59

relation and displayed strong species–environment correlations for the first two axes ($r = 0.81$ and 0.79 respectively; Figure 6). Edaphic variables along with sal and *Mallotus* density and BA as physiognomic variables explained their significance as important variables. The distribution and association of species were strongly related to the soil temperature at axis 1 and pH at axis 2. While GII was associated with high soil moisture, GIII vegetation was correlated with high soil temperature. The vegetation of GI was related with high pH.

Discussion

Declaring a forest as protected and excluding any interventions is based on the assertion that it is the best way of conserving existing biodiversity and increasing its heterogeneity in terms of structure and species diversity. Results of the study suggest: (a) forests are species poor with low species turn-over (Table 3); (b) most of the species richness is attributable to infrequent species (Table 1) and forests are characterized by the dominance of only a few species; (c) species richness was high for groups which had medium size trees (Figure 2), and (d) for all the groups there is a wide gap between the seedling, sapling abundance and their conversion to lowest diameter class trees (Table 2 and Figure 2).

Among tropical deciduous forests, moist deciduous forests are species-rich compared to dry deciduous forests[12,24]. However, the investigated sal forests are species-poor, *H*′ was evidently less compared to several other sal forests[12]. From different sal forests, Uma Shankar[25] reported *H*′ of 3.59 (156 species), whereas Pandey and Shukla[12] reported *H*′ of 3.96 (208 species). Recently, Kushwaha and Nandy[24] enumerated very high species richness (477 species) from moist sal habitats compared to dry habitats (117 species). Timilsina *et al.*[26] reported 131 species from moist sal forest at Nepal. Altogether, 130 species were recorded from Doon forests in the earliest study[17]. However, in the present study almost half of the species was not recorded despite the ban on silvicultural activities aimed to reinstate key ecological factors expected to increase species richness and diversity. Seth and Bhatnagar[17] reported 35 tree species in these forests, lower canopy highly developed and rich (23 species) compared to top canopy (8 species). Few other studies reported 72–93 species in the tree layer from other sal-dominated forests[12,25]. However, from moist deciduous sal forests, Timilsina *et al.*[26] recorded only 21 tree species. Banda *et al.*[6] reported 218 tree species from Tanzania dry deciduous forests. Kushwaha and Nandy[24] reported 134 tree species in moist sal forest. The present investigation recorded only 11 tree species in the mature stages (see Supplementary Information, Table S1, online).

Overall groups were dominated by only a few species (see Supplementary Information, Table S1, online). In the top canopy sal was the only dominant species and in the lower canopy it was predominantly *Mallotus*. Low *H′* for tree layer (Figure 3), relative BA and sal density underpin the observation (Table 2). Conversely, most of the diversity and richness is the result of rare species, especially shrub and herb layers (Table 1). Low Simpson's index which characterizes concentration of dominance (*Cd*) corroborates this (Figure 3 *b*). Further, high evenness index for understorey layers illustrates that most species are relatively rare[25]. During the course of more than a century until being protected, the forest was worked under uniform and group selection systems, coppice with standards, selection felling and conversion to uniform system. Fairly high number of species reported from an earlier study[17] suggests the influence of forest management practices on species diversity and richness. The reason for this may be both disturbance-resistant and superior competitor species co-existing at those sizes, frequencies and harvesting intensities[3] with many species persisting as intermediate species[1]. An array of microsite conditions created after harvesting allows species of all types to occupy the habitat; selection cutting and shelterwood cutting releases the constrained resource competition and increases the resource availability, enhancing diversity, richness as well as regeneration. On the other hand, less species richness in the current survey shows elimination of disturbance-resistant species from the forests after the omission of silviculture treatments[3]. Elliott and Knoepp[9] suggest that shelterwood and/or selection cuttings are less intensive compared to clear cuttings and assert that diversity was greater following less intensive cuttings than clearcuts and uncuts. Torras and Saura[3],and Battles *et al.*[5] observed positive effect of selection cutting in the form of increased species diversity and richness in contrast to negative effect of clear-cutting on species richness.

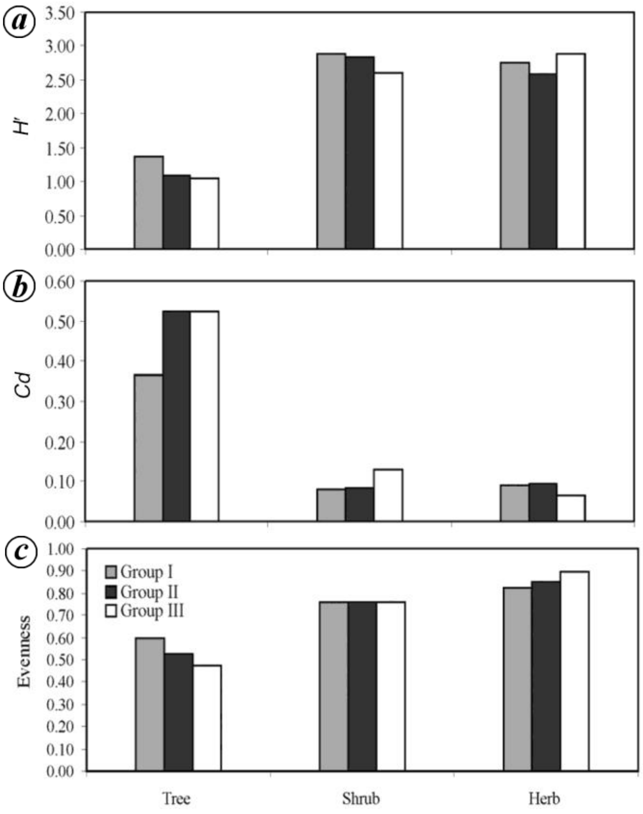

Figure 3. Diversity indices for different groups in tree, shrub and herb layers. (***a***) *H′*; (***b***) Cd; (***c***) Evenness.

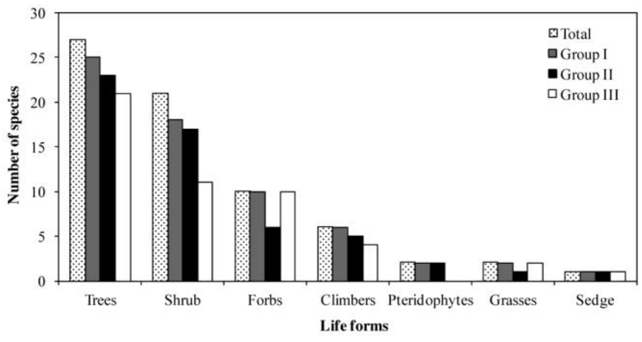

Figure 4. Diversity of life-forms in the ground layers for different groups.

Average tree density was well within the reported densities from the sal forests for GI (404/ha), whereas it was higher for GII and GIII (710–1029/ha) compared to other sal-dominated forests. Uma Shankar[25] reported 484 trees/ha, and Pandey and Shukla[12] reported 402 trees/ha. From Nepal terai region, Timilsina *et al.*[26] reported only 220 trees/ha. Total tree BA of 15.5–28.6 m^2/ha in these forests was within the range reported in earlier studies for the region[27,28] and from other sal forests[12,25,26]. Tree density was a function of mainly sal in GI and GII, where its contribution was more than half towards the total tree density (Table 2). Although within GI and GII sal had overriding contribution towards total density and BA, overall GI and GII had less tree density and BA compared to GIII. Higher BA in GIII is due to higher density of *Mallotus* (see Supplementary Information, Table S1, online) and mature and/or over-mature tree crops (Figure 2 *b*). *Terminalia* in the group within the higher girth class underscores this (Figure 2 *d*). Among trees, sal has the highest BA (see Supplementary Information, Table S1, online). About ≥ 68% of TBA was represented by sal alone, except for GIII, where its contribution was equal to *Mallotus*. This is because of the low density of sal in this group (Figure 2 *a*). Dominance of sal in the top canopy, either in terms of density or BA, or both, was reported unanimously earlier[24–26]. Pandey and Shukla[12] reported sal contribution >80% towards total density and BA. Among understorey trees, *Mallotus* as the most dominant tree was reported as characteristic of Doon sal forests[27,28]. Its dominance in the understorey was also underscored from other sal forests[12,25].

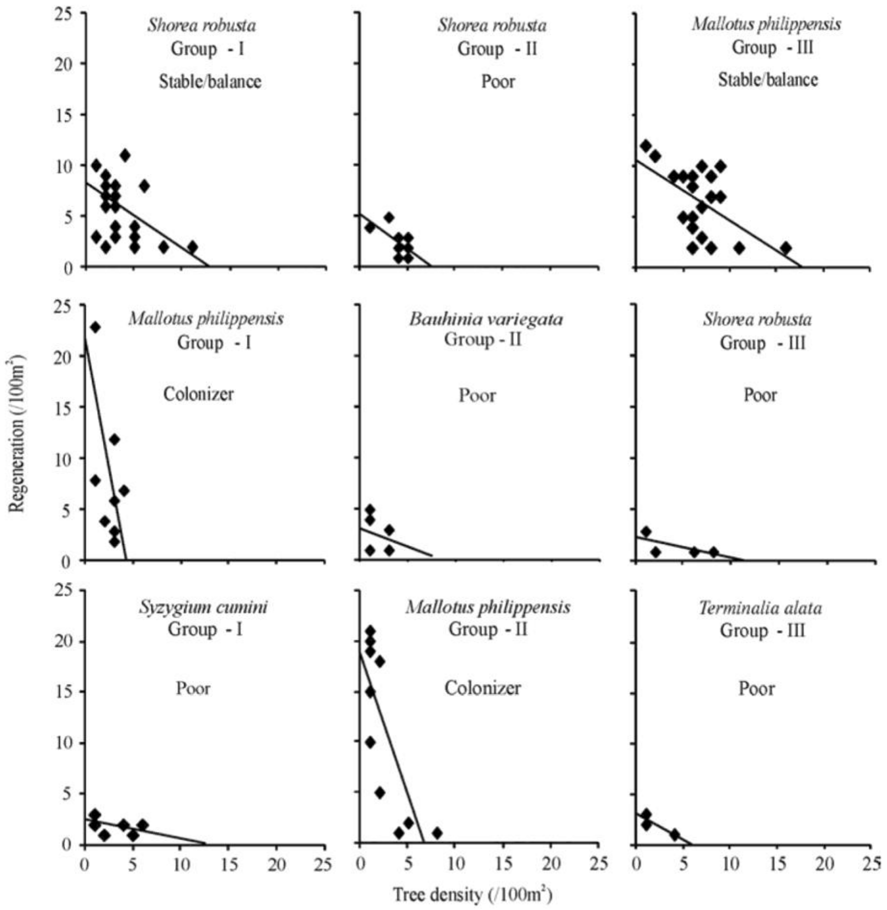

Figure 5. Regeneration trends of the top three species (from top to bottom) of each group based on the relationship between density of seedlings or saplings and adult trees per plot (100 m^2). Three trends, viz. stable/balanced, gap colonizer and poor regeneration were identified.

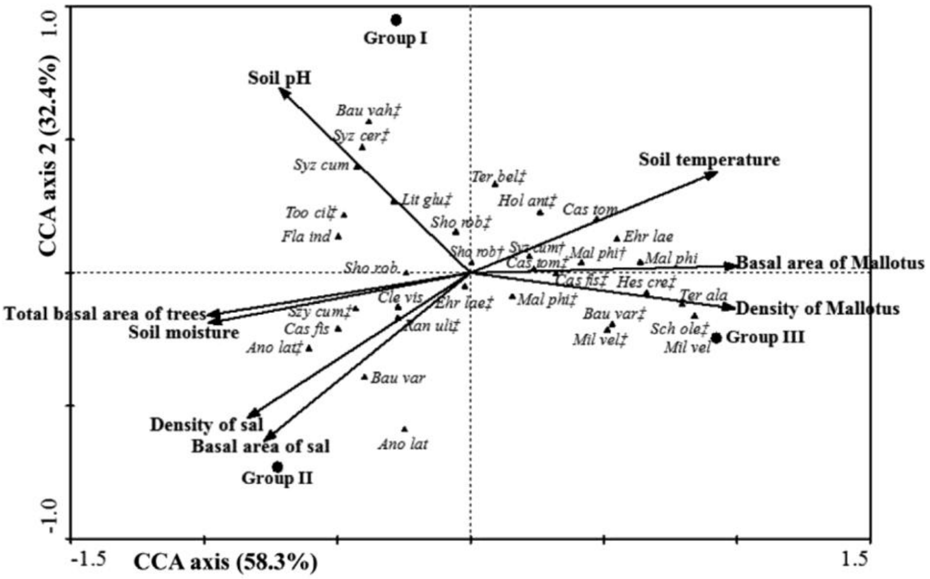

Figure 6. CCA ordination diagram for groups (•) and environmental variables (arrows). The canonical ordination axes 1 and 2 explain 100% of cumulative percentage variance of species environment relation (Monte Carlo permutations test: $f = 6.5$ and $P < 0.05$). Symbols † and ‡ following the species names are for seedlings and saplings of tree species respectively. For complete names of the species see Supplementary Table S1, online.

Concurrently, species richness and diversity increased with a decrease in tree density and BA; GI having the lowest tree density recorded the highest number of species, whereas GIII having the highest tree density recorded the lowest species richness (Table 2). Many infrequent species appeared to decrease in GIII (Table 1). This indicated that stand type (Figure 2; Table 2) with different cover percentage (density and BA) and association are the predominant factors determining species richness. Pandey and Shukla[12] reported the same effect. However, results of Timilsina *et al.*[26] were in contradiction with the general pattern of these forests. This was because of the high disturbance prevalent in the forests they studied. A recent study[24] discussed the same effect of higher tree density on diminished species richness. Sal accounted for total canopy cover primarily in GI and GII, with residual cover provided by *Syzygium* and *Mallotus*. In GII, subcanopy as residual canopy was supplemented by *Bauhinia* and *Cassia* (see Supplementary Information, Table S1, online). In GIII, majority of subcanopy was provided *Mallotus* (see Supplementary Information, Table S1, online). This forms continuous canopy in these forests leaving only a few gaps, especially in GIII. Species which were not encountered in GIII or were less abundant may have been susceptible to the altered microclimatological conditions via changed canopy architecture. However, there was a large variation in the density of species among various communities. For example, climbers were dominantly associated with GI and GII, but with diminished density in GIII (see Supplementary Information, Table S1, online). Schnitzer and Carson[29] compared closed canopy and canopy with gaps, which suggested that gaps are important for the maintenance of climber diversity. Species particularly associated with GI and GII mostly are shade-loving, including understorey small trees *Falcourtia indica* and *Cassia fistula* and shrubs such as *Clerodendium viscosum*, *Flemingia chappar* and *Desmodium pulchellum* (see Supplementary Information, Table S1, online), supposedly associated with late successional stages when canopy cover is optimum. However, diminished density of these species in GIII suggests that they cannot withstand intense shade conditions.

Communities extracted in the study were different for the associate species in GI and GII and completely different in GIII. Cluster analysis illustrated *Mallotus* and *Bauhinia* as sal associates in GI and GII respectively (Figure 1). Sal dominance had been underscored in the preceding section, but *Mallotus* imparting a distinguishing character to the communities was never reported, despite appreciation of it being a dominating tree species of the lower canopy[17,18,26]. The lower number of plots under GIII suggests that this is a relatively recent phenomenon. It may have resulted due to the colonization of early successional *Mallotus* (along with *E. laevis*) to the wide canopy gaps created after the heavy sal mortality[28]. Low sal density under this group underpins this fact. Gautam *et al.*[30] have also stated that *Mallotus* colonizes the gaps because it is better adapted to less soil moisture conditions, which were created due to canopy openings. It propagates efficiently through coppicing, ramet production and enormous seed production, especially when gaps are prevalent. It is a facultative sciophyte, which grows best under elevated light levels, but can also grow equally well under shade and can tolerate frost, drought and disturbance[31]. Frost is a common occurrence in Doon Valley and sal juveniles are frost-susceptible. As a result, when appreciable gaps exists sal recruits dieback, which is a common phenomenon and compensatory effect leads to the dominance of *Mallotus*. Its advanced regenerations are bushy in nature that helps conserve moisture, which is good for sal regeneration. This was reinforced in the present study by a good number of sal seedlings within this group (GIII; see Supplementary Information, Table S1, online). However, pole stages to lower diameter class sal trees were not recorded from this group (Figure 2). This may be due to disturbance in the form of grazing–browsing and forest fires and/or to progress further, sal establishments are strong light-demanders which cannot withstand enhanced moisture regime[32]. High tree density and BA (Table 2; see Supplementary Information, Table S1, online) suggest that canopy is almost continuous which is an impediment for further advancement of sal juveniles to subsequent stages. Seth and Bhatnagar[17] underlined the adverse effect of *Mallotus* on sal seedlings and saplings, citing it as negative indicator of natural regeneration and establishment. Similarly, for *Syzygium* good number of seedlings was recorded but diminished conversion to saplings and no pole or tree in lower diameter class was seen for this group (Figure 2 *c*). Although *Syzygium* is a shade-tolerant species which effectively withstands excessive moisture conditions, seedling and saplings are fire- and grazing-susceptible. High *Mallotus* seedlings and saplings, with their progressive conversion to higher diameter class (Figure 2), illustrate that both sal and *Syzygium* juvenile stages are outcompeted by *Mallotus* for resources within this group. Also, *Mallotus* can withstand the disintegrating regimes more effectively, which other species in these forests are found susceptible. According to Seth and Bhatnagar[17], *Mallotus* successionally precedes sal and establishes itself successfully outcompeting other species and ultimately acts as a nurse crop whenever sal recruitments start colonizing the sites. However, Figure 2 contradicts this hypothesis. First, *Mallotus* in this group belongs to mature class and second, sal trees are always seen in the group, though less in numbers, with high turnover of seedlings and saplings. This illustrates the competition (for resources) sal is facing in these plots.

CCA showed that soil temperature and moisture strongly influence the distribution of groups and their composition. GIII was closely associated with the high soil temperature (Figure 6). These factors have become important due to canopy openings in the recent past[28]. A shift in energy balance cascades into altered soil temperature and evapotranspiration rates[31] when overstorey is removed and high order of radiant energy reaches the forest floor than what infiltrates through intact canopy[14]. The changing soil temperature and correlated changes in edaphic factors can alter patterns in plant recruitment via differential effects on propagules and subsequently affect the composition within the community. This effect was more evident in GIII, where *Mallotus* had gained dominance over sal. Most of the earlier studies had appreciated soil moisture as the important environmental variable[23] along with canopy opening[17] for the moist deciduous forests. Gautam *et al.*[30] also reported soil moisture as the most important environmental factor for sal forests at various stages, especially at seedling stage. But with the changing canopy cover, a detailed study on the interaction between soil temperature and community distribution is required.

Studies revealed that seedlings were sufficiently produced but their establishment was a problem. Impaired regeneration progression of tree species, including that of umbrella species in these forests is presenting a challenge to biodiversity conservation efforts. Within tree life-form, 13 species were represented as juveniles only (see Supplementary Information, Table S1, online). For them to proceed further they need space and other resources. Several tree species recorded in sapling stages were concurrent with those recorded by Seth and Bhatnagar[17]. This illustrates the fact that these forests are trying to regain the original configuration. However, a few new species reported in juvenile stages in the present study were not reported by them. This shows that forests are providing habitat to disturbance-resistive species and/or species which establish themselves as shade-tolerant. To rectify this, in GI, saplings need protection in the initial stage of establishment. Since tree density of the group was 404 trees/ha, retention of an adequate cover of miscellaneous middle-storey species would help in moisture retention. For GIII, seedling to sapling conversion rate was satisfactory, but complete absence of 6–15 and 16–25 cm diameter trees is a matter of concern. This probably was due to high tree density (1029 trees/ha). With some modifications to the overall forest structure, forest managers could expect the growth stages of sal and associate species to improve. The population structure of GII and GIII suggests that removal of overmature trees with saplings protection will certainly improve the low density of sal trees between 6 and 45 cm diameter. Following the harvest of mature trees, younger size classes will respond with a larger growth increment, due to more favourable light conditions[3]. For this, selection harvesting is an alternative, where snags, diseased, malformed, advance growth and overmature trees should be selectively removed. Merits of this approach are that it will not affect the present seral stages, but will create gaps to initiate only gap-phase regeneration[8,29]. Moreover, compared to the overstorey canopy cover which is maximally a function of sal, the understorey is structurally and climatically more diverse. Selectively removing old large will not disrupt (abruptly) canopy cover and the uniformity of biogeochemical/physical conditions significantly, but will simultaneously create spaces for regeneration. However, for tropical forests, where several strata are available, reduction in the density of understorey is as important as overstorey structure. Even if structural changes are made in the overstorey, high density and cover offered by the understorey vegetation will thwart tree regeneration within the gaps. On the contrary, any manipulation in the overstorey in this scenario would help understorey to develop profusely[9]. In addition, gaps help maintain and/or increase diversity by providing increased light and space for regeneration as well as colonization for both shade-tolerant and shade-intolerant communities[3,7,8,29]. Here, size of the gap is of principal importance. While small gaps were seen increasing the diversity and structural attributes in the initial years[8,29], large gaps resulted in setting up new successional stages based on the few light-demanding and dominating species in the earliest stage leading in low species richness[3] and impaired regeneration[28]. Chauhan[28] reported the profuse growth and density of *L. camara*, an invasive weed, in these forests, attributed to the excessive opening of canopy, leading to very low species diversity for the patches where *L. camara* occurs and complete absence of regeneration in the vicinity.

Low species richness and turn-over indicate that forests are species-poor (see Supplementary Information, Table S1, online) which bears directly on the biodiversity conservation of such forests. These forests, which are critical habitats for herbivores, birds and butterflies, need conservation for their plants, animals and their interactions. Silvicultural operations varying in size and intensity which eventually increase the distinctiveness of microenvironment available for regeneration, establishment and growth are needed for forest management. Thus, a complete abandonment of harvesting and other manipulations as management options for the forests need not necessarily induce species diversity as well as regeneration of species. Previous studies emphasized similar effect of protection resulting into lower species richness[3,5]. Banda *et al.*[6] reported similar results for forests where management plans disallowing change in structure resulted in the lowering diversity compared to forests worked under management plan. Results of the present study illustrate that decision of omission of silviculture related interventions is not an appropriate management strategy of enhancing species diversity, regeneration and conservation of these forests. After an initial period of restitution for forests which experienced intensive management practices, it is desirable to emulate the conditions of intermediate disturbance through moderate stand, improvement cutting or selection cutting. Torris and Saura[3] showed that the forest species diversity, regeneration and structure would benefit from moderate intensity forest management strategies falling under intermediate disturbance conditions. Intermediate intensity disturbances create a non-equilibrium situation that brings micrometeorological variation and subsequent increase in species diversity by providing an opportunity for the fast colonizing and pioneer species to establish in a community according to the conditions they create[1].

Forests are declared protected primarily to keep the health of forest ecosystem intact, so that potential benefits from them could be maximized. It is also asserted that conservation of flora appropriately helps in conserving biodiversity, inclusive of faunal diversity. To achieve biodiversity conservation objectives, within the constraints of proscription, forest managers should alter the distribution and/or spatial scaling of biotic and abiotic factors to maintain or reinstate key ecological processes. This would help in the regeneration and establishment of viable species population to underpin both species richness and sustainable timber production.

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