Patterns of diversity and regeneration in unmanaged moist deciduous forests in response to disturbance in Shiwalik Himalayas, India

Mukesh Kumar Gautam a,*, Rajesh Kumar Manhas b, Ashutosh Kumar Tripathi a

aForest Ecology and Environment Division, Forest Research Institute, Dehradun, India
bDepartment of Botany, Government Degree College, Kathua 184104, Jammu and Kashmir, India

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ABSTRACT
We studied vegetation attributes in Indian tropical moist deciduous unmanaged forests to determine the influence of forest disturbances on them. We enumerated 89 species: 72 under moderate disturbance and 54 under least disturbance. The data from 3399 stems [3–5 cm diameter at breast height (dbh)] decreased linearly along the disturbance gradient. The basal area was largest in least disturbed forests (61 m²/ha) and smallest in intensely disturbed forest (41 m²/ha). Under least and moderate disturbance, tree density−diameter distribution had negative exponential curves, whereas highly disturbed forests had unimodal-shaped curves where a few trees 5–10 cm and >50 cm in diameter were recorded. Most tree and shrub layer species under heavy and intense disturbance had impaired regeneration. Moderate disturbance intensity thus apparently benefits species diversity, stand density, and regeneration. Decline in seedlings and saplings, especially tree species, threaten forest regeneration and the maintenance of species diversity of unmanaged tropical forests.

Introduction
Several factors at different spatial scales influence species diversity, composition, and structure of tropical forests (Peña-Claros et al. 2012). On the regional and local scale, diversity and structure are strongly influenced by natural and anthropogenic disturbances (Wright 2005; Peres et al. 2006; Sheil and Burslem 2003). The relationships between disturbance with plant diversity, composition, structure, and regeneration have been discussed in many studies. Natural and anthropogenic disturbances are critical to plant diversity, structure, and regeneration of forest ecosystems (Pandey and Shukla 2003; Sagar et al. 2003; Mishra et al. 2004; Zhu et al. 2007) because both forms of disturbance alter environmental conditions, ecosystem processes, nutrient availability, and plant−plant interactions (Sheil and Burslem 2003; Walker 2012). Empirical studies show that, as the frequency and intensity of disturbance increase, plant diversity and other associated vegetation attributes decrease (Peltzer et al. 2000; Sapkota et al. 2009; Takaﬁmi and Hiura 2009; Pretto et al. 2010; Mayor et al. 2012). This phenomenon occurs because only a few disturbance-resistant and/or disturbance-tolerant species can persist under intense and frequent disturbance (Roberts and Gilliam 1995). Connell (1978) postulated that as disturbance increases, species diversity should also increase to the point of intermediate disturbance intensity, size, and frequency because disturbance-resistant and superior competitor species can coexist with many species persisting as intermediate species in various stages of recovery. In particular, several field-based studies from tropical and temperate forests report that species richness, diversity, and regeneration peak at intermediate disturbance and decrease beyond that point (Hobbs and Huenneke 1992; Peltzer et al. 2000; Molino and Sabatier 2001; Bongers et al. 2009; Mayor et al. 2012). By contrast, other studies report noncompliance to the intermediate disturbance effect on species diversity (Shea et al. 2004; Kershaw and Mallik 2013). A significant increase in anthropogenic disturbance and coupled ongoing biodiversity loss necessitate learning about the relation of disturbance with species diversity, structure, and regeneration.

In general, in most fragmented tropical forests, a very large network of reserve forests has been created that is unmanaged or under protection. The motive of this exercise is postdisturbance forest (i.e. vegetation) recovery by weakening disintegrating forces inimical to the forest structure and diversity. Despite protection and
all best efforts to conserve biodiversity, tropical forests experience anthropogenic disturbance. The intensity and frequency of anthropogenic disturbance change periodically. Large-scale felling may not occur, but several small-scale intensive and frequent disturbances (e.g. pruning and lopping for fuel wood and fodder, grazing, browsing, and fire) occur, which may have similar effects as large-scale felling on diversity and structure. Several studies report the prevalence of ancillary disturbances (e.g. pruning, lopping, fire, grazing, and browsing) in protected and reserve forests and their simultaneous impact on plant species diversity, stand structure, and forest regeneration (Muthuramkumar et al. 2006; Torras and Saura 2008; Sapkota et al. 2009).

With increasing anthropogenic disturbances and consequent transformation of tropical forests, even in protected/reserve forests (Muthuramkumar et al. 2006), it has become imperative to assess whether such areas realize their goal of biodiversity conservation. The prioritization and realization concerning the conservation potential of protected forests would evidently benefit from diversity-disturbance studies from tropical forests. This factor needs further elaboration because the effects of different disturbance levels on diversity, structure, and regeneration of unmanaged forest are deficient, if not missing. Hence, the diversity-disturbance debate needs further work in unmanaged forests. With the increasing conservation of such optimal zones can be prioritized under scenarios of anthropogenic disturbances. Because of the lack of disturbance studies focusing on unmanaged forests, this study was undertaken to provide a disturbance index for moist deciduous unmanaged forests, to characterize the compositional and structural changes along various disturbance intensities (Ds), and to explore the relationship of these intensities with the change in species diversity, structure, and regeneration. We anticipated that in protected forests, which are now unmanaged, disturbances should be concentrated on lower diameter at breast height (dbh) trees or lower story trees. We further anticipated that the effect of disturbance would be distinctive for different tree layers and different vegetation layers. We further anticipated that the least and mild disturbances had a moderating effect on diversity, structure, and regeneration of unmanaged forests.

**Material and methods**

**Study site**

This study was performed in four forest ranges of moist deciduous forests in Shiwalik Forest Division (Dehradun District) of India (29°55’ and 30°30’ North and 77°35’ and 78°24’ East), which is dominated by late successional *Shorea robusta* (Sal) (Figure S1). Elevation of the study region ranges 600–800 m above the mean sea level. The region has a humid tropical monsoon climate with three seasons: hot and humid summer (March–June), hot and humid rainy season (July–September), and winter (October–February). Annual temperature ranges from 18.6°C (in January) to 40.0°C (in June). The region receives average annual rainfall of 2,025.43 mm, the bulk of which is received during the rainy season from June to September. The study forests were growing on the alluvial piedmont plain, which consists of deep, medium to moderately fine-textured, well-drained loamy soils belonging to Inceptisols and Alfisols. Epipedon showed feeble O-horizon and A-horizon with a less dense litter layer, especially at sites that were heavily disturbed. The soil pH was moderately acidic (5.34–6.46). The percentage of organic carbon was 1.02–2.70%. Organic matter was in the range of 2.50–5.74%. The total nitrogen and available nitrogen were 0.08–0.19% and 0.01–0.03%, respectively. Cation exchange capacity ranged from 18.37 cmol (p+)/kg to 9.97 cmol (p+)/kg. The exchangeable calcium ranged was from 5.58 cmol (p+)/kg to 3.96 cmol (p+)/kg. The exchangeable magnesium ranged from 4.38 cmol (p+)/kg to 2.79 cmol (p+)/kg, and potassium ranged from 0.67 cmol (p+)/kg to 0.42 cmol (p+)/kg.

Forests in the Shiwalik belt have a long history of disturbance. Their natural distribution was radically altered in the past 150 years of disintegrating anthropogenic interventions (Appendix S1). In 1980, these forests were classified as reserved forests through enactment of conservation laws to halt the recede in their cover and reinforce conservation. Despite protection, anthropogenic pressures on these forests are increasing in the form of expanding habitation, illegal harvesting, lopping, grazing, forest fires, tourism, and industrial expansion. Human population increased by 1123% and density by 900% during the past 130 years in the region. From 1880 to 2001, arable land increased from 41,000 ha to 709,740 ha and livestock population increased from 168,000 animals to 887,918 animals.

**Sampling design, data collection, and disturbance assessment**

In each of the four forests, 10 sample plots of 0.1 ha were established. Within each plot, 10 quadrats of 10 m × 10 m were laid to inventory the tree layer. Within the center of each 10 m × 10 m quadrat a 3 m × 3 m quadrat and a 1 m × 1 m quadrat were nested to inventory shrub and herb species composition and diversity. Plants were assigned to different layers, based on their height and diameter: trees > 5 cm dbh, shrubs (and woody species) > 1.0 m in height and/or 1.5–5 cm in diameter, and herbs (all species) < 1.0 m in height and/or < 1.5 cm in diameter. Saplings (i.e. trees) were included in the shrub layer, whereas seedlings (i.e. trees and shrubs) were included in the herb layer. In every quadrat, the number of individuals (for abundance) and the diameter of each species were recorded. For trees, the diameter at breast height (dbh) was obtained, and for shrubs and herbs, the collar diameter was measured.

Various prevailing influencing and causative disturbance factors were identified and their intensities were recorded. The major disturbances (i.e. causative factors) in these forests were grazing, browsing, fodder/fuel wood cutting/lopping, fire, and insect attack. The influencing factors (i.e. factors that influence the frequency and intensity of disturbances) that were included in devising the Ds were distance from a road, distance from human settlements, and distance from agriculture and tourism. All disturbances were anthropogenic, except for insect attack and grazing (which include wild animals). Disturbance intensities for various forests were estimated in accordance with the method of Sagar et al. (2003) and Zhu et al. (2007). A site that was at the maximum distance from a road, agricultural land, habitations, or recreation spots was assigned intensity 1 (i.e. minimum intensity). The intensities for the other sites were calculated as the ratio of the distance of site to the distance of other sites. For instance, the criterion for adjudging the site disturbance intensity is the maximum values for the disturbance factors (i.e. 9,000 m, 9,140 m, 8,921 m, and 8,789 m) for a site’s distance from a road, habitations, agricultural and tourism spots respectively (i.e. impact factor 1). The nearest distance of a site from a road, habitations, recreation spots, and agricultural land was 300 m, 330 m, 300 m, and 320 m, respectively. Thus, the highest impact factor for road (9000/300), habitations (9,140/330), tourism spots (8,921/300), and agricultural land (8,789/320) were 30, 27.77, 29.73, and 27.46, respectively. Cutting/lopping and insect attack intensities were similarly calculated by the relative trees affected (%) and that of GP (grazing pressure). Fire intensity was assessed from the forest records; the relative trees affected (%) and that of GP (grazing pressure) by cutting/lopping and insect attack intensities were similarly calculated by the relative trees affected (%) and that of GP (grazing pressure). Fire intensity was assessed from the forest records; the relative trees affected (%) and that of GP (grazing pressure) by cutting/lopping and insect attack intensities were similarly calculated by the relative trees affected (%) and that of GP (grazing pressure).

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with very old fire incidences were categorized as intensity 1 because we were uncertain about their impact on the present vegetation.

After summing the intensities, four forests had average disturbance scores of 14.6 [disturbance-I (D-I)], 35.0 [disturbance-II (D-II)], 57.0 [disturbance-III (D-III)], and 58.2 [disturbance-IV (D-IV)] (Table S1). In the discriminant analysis (i.e., Wilks’ \(\lambda - F = 14.96; p < 0.0001\) ), the standardized discriminant coefficients and centroid positions showed that forest stands were significantly different from each other with respect to their DICs (Tables 1 and S1). The multidimensional Mahalanobis distance, which is invariant to changes in the scale of variables (Digby and Kempton 1987), was statistically significant (\(P < 0.01\)) for all pairwise distances between sites. Discriminant function-1 (DF1; 60.88% variance) separated heavily disturbed sites (i.e. D-III (3.65) and D-IV (3.79)) from less disturbed sites (i.e. D-I (2.23) and D-III (2.75)), whereas discriminant function-2 (DF2) (32.38% variance) separated D-I (3.53) from D-II (2.75). The distance measure between D-III and D-IV, despite being small, was significant (\(P < 0.001\)). The first two discriminant functions (i.e. DF1 and DF2) significantly discriminated different forests from each other (\(P < 0.0001\): Figure 1). The canonical correlation was very high (\(> 0.92\)) and significant (\(P < 0.05\)) among different forests, and DF1 and DF2 indicated the ability of canonical functions to explain the differentiation between forests (or intensities; Table S1). In DF1, negative standardized coefficients of distance from agriculture and cutting/lopping indicated that increased distance from agricultural fields was associated with the negative direction along this function. This was confirmed by the forests (i.e. D-III and D-IV) toward the positive end of the function, which had higher DICs than the remaining two forests on the other function. Further positive coefficients of distance from road (i.e. DF 1) and distance from habitation (i.e. DF2) confirmed this.

**Diversity measurements and data analysis**

Importance value index of each species was calculated, based on the relative values of its frequency, density, and basal area (BA). Five diversity indices—species richness, Shannon diversity (\(H'\)), Simpson’s index (\(C'\)), Jaccard index of similarity, and Pielou’s evenness (\(J'\))—were calculated, based on the method described by Magurran (1998).

Variation in the DI, species richness, and diversity and evenness indices was determined by analysis of variance; this was followed by individual comparisons of the mean using Fisher’s least significant difference (\(P < 0.05\)). The effects of the DI on various diversity attributes were modeled by general linear regression (XLStat-Pro; Addinsoft, New York, NY, USA).

**Results**

Least disturbed forests (i.e. D-I) and moderately disturbed forests (i.e. D-II) were different in species diversity, stand density, BA, and tree size classes, compared to other disturbed forests (Figures 2–4). Moderately disturbed forest had 1.18–1.33-fold more species, 1.21–1.38-fold more families, and 1.20–1.33-fold more genus richness, compared to other forests, and contained 80% of the total species recorded from all the forests (Tables 1, S2, and S3). Tree and herb species richness were highest in D-II and lowest in D-IV, whereas shrub species richness was highest in D-IV and lowest in D-I. Unique species (i.e. regime-specific species not present in other intensities) were highest in moderately disturbed forest (D-II; 10 species), and least in heavily disturbed forest (D-IV) (Table 1). Relatively few species were common among all forests, eight trees, nine shrubs, and five herbs.

**Figure 1.** Linear discriminant biplot for the first two discriminant functions with centroid positions and Mahalanobis distance (D2) measures among forests. The D2 (numerical values) and probability values (\(P < 0.001\)) shows the extent of disturbance dissimilarity between different disturbed forests. D-I, forests with an average disturbance score of 14.6; D-II, forests with an average disturbance score of 35.0; D-III, forests with an average disturbance score of 57.0; D-IV, forests with an average disturbance score of 58.2.

**Figure 2.** Box and whisker plot of Shannon diversity (\(H'\)), concentration of dominance (\(C'\)), evenness, and Jaccard similarity of the tree layer, shrub layer, and herb layer in different disturbance intensities in Doon Valley forests. Horizontal lines within the boxes indicate the mean values; the upper and lower boundaries of the boxes indicate the standard deviations; and the whiskers span the ranges of individual values measured. Lowercase alphabetical letters indicate the post hoc multicomparison Fischer’s least significant difference results (\(P < 0.05\)). D-I, forests with an average disturbance score of 14.6; D-II, forests with an average disturbance score of 35.0; D-III, forests with an average disturbance score of 57.0; D-IV, forests with an average disturbance score of 58.2.
With regard to diversity indices, different vegetation layers showed variations in the effect of disturbance (Figure 2). The maximum and minimum Shannon diversity for the tree layer corresponded with moderately disturbed (i.e. D-II) and severely disturbed forests (i.e. D-IV), respectively (Figure 2A). Tree Shannon diversity decreased significantly with increasing intensity ($F = 13.06$, $P < 0.001$; Table 2). Highest and lowest Shannon diversity in shrub and herb layers was under D-II and D-IV, respectively, but for herb layer difference among various disturbed forests was not statistically significant ($F = 0.5$, $P = 0.90$). Simpson index illustrating the concentration of dominance was lowest in the least disturbed forests and highest in severely disturbed forest for tree layer (Figure 2B). Tree Simpson index increased significantly with increasing disturbance intensity ($F = 11.20$, $P = 0.002$; Table 2). The Simpson index of the shrub layer differed significantly among disturbed forests (Figure 2F), but regression analysis revealed that the relationship of the Simpson index with the disturbance intensity was insignificant ($F = 3.47$, $P = 0.07$), although the correlation was significant (Person’s coefficient, $-0.34$; $P = 0.04$). In least disturbed forests, tree species were more evenly distributed than in other highly disturbed forests, whereas shrub species were more evenly distributed in moderately disturbed forests (Figure 2). However, for the tree layer, the relationship between evenness and DIs was insignificant. The Jaccard index of the similarity of the tree layer was lowest in D-I and highest in D-IV ($F = 4.3$, $P = 0.01$), but it did not vary significantly in the shrub layer and herb layer among the different forests (Figures 2H and 2I).

Probabilities corresponding to an $F$ value lower than 0.05 indicate that disturbance significantly affects various diversity indices and density attributes (Table 2). Disturbance had a significant inverse effect on tree species richness (slope $-0.09$; $P < 0.0001$). However, the relationship between the disturbance intensity and change in the species richness of the shrub layer (slope $0.11$; $P = 0.001$) and the herb layer (slope $0.07$; $P = 0.003$) was positive and significant. There were no differences in the Shannon diversity of the shrub and herb layers (intercept $1.92$ and $1.87$, respectively); both increased (slope, $0.004$ and $0.006$, respectively; $P < 0.05$) with the decrease in tree Shannon diversity (slope, $-0.01$; $P = 0.001$).

The total number of stems recorded in all forests was 3399; of these, 60% (2029) of stems were recorded in the least disturbed forests (1120 stems) and in moderately disturbed forests (909 stems). The number of trees varied 2–23 per quadrat (10 m × 10 m). The number of quadrats with > 10 trees was highest in D-I forests (3.4-fold higher), compared to other disturbed forests. The total tree density was higher in least disturbed and moderately disturbed forests than in heavily disturbed forests (Figure 3A). Overall stand tree density when separated into overstory and understory showed a pronounced effect of disturbance in the understory tree layer in intensely disturbed forests, compared to least disturbed and moderately disturbed forests (Figures 3B and 3C). To this end, a significant difference in the BA between various forests was evident (Figure 3D–F). In addition, with regard to different tree layers, BA decline was more abrupt in overstory trees than in understory trees. The density pattern of the shrub and herb layers was different from the density pattern of the tree layer. The shrub layer showed a quadratic relationship for density and for the BA. Shrub...
density was highest in moderately to very disturbed forests than in least disturbed and severely disturbed forests.

The shape of the size-class distribution was different among the various forests. Least disturbed forests had a different size-class distribution than other disturbed forests (Figure 4). Least disturbed forest had 1.6–2.8-fold more trees and 1.07–2.3-fold more BA in the size-class 5–20 cm, compared to other forests (Figure 4). In severely disturbed forests, few trees were 5–10 cm or >50 cm in diameter. The same pattern also occurred for BA’s. The density and the BA of trees >50 cm (i.e., adult trees) decreased linearly ($R^2 = 0.99$ and $R^2 = 0.96$, respectively) from least disturbed to severely disturbed forests. Sal density increased linearly as the DIs increased ($R^2 = 0.99$); severely disturbed forests had 1.72-fold more trees than least disturbed forests with a BA 1.15-fold higher than that of least disturbed forest. An inverse relationship existed between density-size diameter classes; however, the relationship differed between disturbed forests (Figure 4). For least disturbed forests, the relationship was quadratic ($F = 36.71, P = 0.0005$); however, for the other forests, the relationship was of an order greater than two ($F = 5.53–17.40, P = 0.05–0.004$).

A simple assessment of tree species presence—absence revealed that, except for Sal, no other species was present in all 40 of the 0.1 ha, whereas the second most dominant tree, Mallotus sp. was present in 29 plots of the 0.1 ha size. Further analysis showed that Mallotus sp. saplings existed in all 40 plots, but Sal existed in only 23 plots. For shrubs and herbs, a generalized pattern was noticed in which the density of most species increased with increasing disturbance intensity. Two species of the shrub layer that existed in all 40 plots were Murraya Koenigii and Clerodendron viscum. Further analysis of most dominant tree saplings in the shrub layer showed an opposite effect of disturbance: Sal sapling density decreased linearly ($R^2 = 0.80$) with the disturbance from least disturbed forests to severely disturbed forests, whereas Mallotus sp. showed a quadratic increase in the density ($R^2 = 0.98$; Table S4).

Approximately three-quarters of the tree species in D-III and D-IV had poor to very poor regeneration (Table 3). For the shrub layer, the maximum number of good regenerating species were found in D-I (54.2%), followed by D-III (38.5%), D-IV (30.8%), and D-II (27.3%). The highest number of very poor-regenerating to poor-regenerating shrub species was in D-I (62.0%), and the least number was in D-II (45.8%). Grasses and sedges showed good regeneration in all forests of different DIs.

## Discussion

It has been empirically shown that anthropogenic disturbances greatly affect biodiversity (Zhu et al 2007; Takafumi and Hiura 2009). Species richness was lower in forests experiencing intense disturbances, compared to forests experiencing mild to moderate disturbances. The pattern was similar to that reported by Mishra et al. (2004), Sapkota et al. (2009) and across different disturbance types (Peltzer et al 2000; Zhu et al 2007; Sahu et al. 2008). Mild and moderate DIs (i.e., the intermediate disturbance hypothesis) creates alternative nonequilibrium conditions that bring change (i.e., increase) in species diversity by providing fast-colonizing species an opportunity to establish within a community (Connell 1978; Robert and Gilliam 1995; Molino and Sabatier 2001). Roxburgh et al. (2004) highlight that species differ substantially in their response to disturbance, and coexistence under intermediate disturbance regimes can arise from fundamentally different coexistence-enabling mechanisms. Disturbances had a distinct effect on the species richness of different vertical layers. Tree and herb species richness decreased significantly with an increase in disturbance. Contrary to this, shrub species richness increased (Tables 1 and 2). The number of species existing as tree sapling and seedling decreased with an increase in DIs, with maximum species accumulation occurring in moderately disturbed forests.

The results of diversity indices (e.g., Shannon diversity, Simpson index, Jaccard similarity, and evenness) suggest an uneven effect of disturbances on different vegetation layers. Shannon diversity and evenness of the tree layer had an inverse trend with increasing disturbance intensity (Figure 2 and Table 2). This is in contrast to...
the results of Peltzer et al. (2000), who stated an increase in Shannon diversity and evenness with increasing disturbance intensity. For instance, the Simpson’s index for tree layer was highest in D-IV, which suggests that intense disturbance drives overstory toward homogeneity. However, the lowest evenness at high DIs reflects that much of the value of the Simpson index is attributable to the elimination of rare species at this intensity. The Simpson index weighs heavily towards most abundant species in the sample and is less sensitive to species having only a few individuals (Magurran 1998; Pandey and Shukla 2003). Sapkota et al. (2009) attributed this phenomenon to the heavy dominance of disturbance-tolerant dominant overstory species in heavily disturbed sites. The shrub layer had the opposite finding: the Simpson index was highest under D-I and evenness was highest under D-IV. In the herb layer, the Simpson index was lowest in D-III, but there was no statistically significant difference in the evenness of different disturbed forests. A low Simpson index for both understory layers reflected that disturbance resulted in low equitability and high dominance because of the incongruent exploitation of species. The Jaccard index for tree layer species showed a low level of similarity between moderately disturbed forests and highly disturbed forests. Low Jaccard similarity values of D-II/D-I forest compared to D-III/D-IV forests suggest that a difference exists in species composition and abundance between them. As many as 11 tree species were limited only to the lowly disturbed forests (D-I/D-II), compared to highly disturbed forests (D-III/D-IV). The remaining species in D-III/D-IV differed strongly in terms of individuals per species. However, the Jaccard index of similarity of other two layers did not show any definite pattern.

Because disturbance is critical to dominance and abundance, fewer species/individuals per unit area in the sampled sites were expected, especially in lower dbh classes.

The total tree density (P < 0.007) decreased significantly along the DIs, which was in agreement with disturbance studies from other tropical forests (Molino and Sabatier 2001) and elsewhere (Zhu et al. 2007). We anticipated that because these forests are protected reserve forests, the disturbance impact on the tree layer could be concentrated more toward lower dbh trees and lower story trees. For the lower story tree layer, the stem density decreased linearly and steeply along the gradient of disturbance (Figure 3). However, in the overstory tree layer, which represents adult trees, the highest stem density was in moderately disturbed forest than in either the least or heavily disturbed forests. The pattern of dbh size-class distribution differed significantly among different forests (Figure 4). Least disturbed forests showed a typical negative exponential curve, a stem density decline with increasing dbh size classes, and undisturbed tropical forests (Ganesh et al. 1996). In moderately disturbed forests, a sharp reduction in the lowest dbh class trees (5–10 cm) was reported. Thereafter, in heavily disturbed forests (D-III/D-IV), along with lowest dbh class trees, the stem density in other dbh classes also declined. These results in severely disturbed forest are not concordant with our assumption that in protected forests, where felling is prohibited, disturbance through illicit felling is limited to lower dbh size-class trees. However, the effect of disturbance was more pronounced in the lower dbh stems of understory tree layer, compared to high dbh adult stems of the overstory tree layer. Sapkota et al. (2009) and Muthuramkumar et al. (2006) also made similar observations of the stem density decline being more pronounced in the low dbh classes than in the high dbh classes. Trees of low dbh classes are preferentially felled because of the ease in illicitly cutting them, which may go unnoticed, and the ease in transporting them out of the reserved forests in comparison to large adult trees.

The effect of disturbance on shrub density and BA was opposite to the effect of disturbance on the tree layer (Figure 3). The shrub layer density and BA increased with an increase in the gradient of disturbance, until an intensely disturbed condition was encountered (Figure 3). Other investigators also discussed a similar dominance of shrub layer, after a disturbance-led gap formation in the canopy (Mishra et al. 2004; Peltzer et al. 2000). Higher light levels and lower stem density of trees, especially of adult trees with dbh > 20 cm could have facilitated the luxuriant growth of the shrub layer. The linear regression of tree density with shrub density recorded a mild inverse effect (slope = −0.10; P = 0.04; Figure 5).

This may be related to the reduction in resource competition (Denslow et al. 1998) and the prevalence of more favorable conditions in the subcanopy environment for shrub layer species to flourish under disturbances (Bongers et al. 2009; Takafuli and Hiura 2009). An interesting component of the shrub layer was the heavy dominance of woody Malolotus philippensis with a collar diameter ranging 3.5–4.8 cm. This could be attributed to heavy cutting, lopping, and pruning because it is a valued fodder and fuel wood species. This is supported by the fact that density of M. philippensis in the tree layer declined linearly from highest in least disturbed forest to lowest in intensely disturbed forest. Part of the reason for high shrub density and BAs in intensely disturbed forest was the presence of woody and shrubby overgrowth of tree species resulting from persistent cutting and lopping. For instance, intensely disturbed forests had a high dominance of Litsea glutinosa, Litsea monopetela, and Ehretia laevis (Table S4).

An increasing dominance of Sal in the tree layer along the increasing gradient of disturbance shows that it had effectively survived the disturbance by devising certain coping mechanism against disturbance. Sapkota et al. (2009) suggested that it had evolved into a stress-tolerant species after remaining under persistent disturbance for a prolonged period. However, in our study Sal sapling and seedling density decreased linearly from least disturbed forests to severely disturbed forests (Table S4). The dominance of adult Sal trees suggests that they effectively withstood disturbance in the past. In recent times, adult Sal trees have not been preferred for illicit harvesting owing to their larger size, which is difficult to transport out of the forest. However, its seedlings and advanced growth may be impacted by grazing, browsing and/or resource competition from M. philippensis dominance (which reproduces profusely asexually via ramet production) and other dominant shrubs (e.g., Clerodendron viscosum) in the shrub layer. The dominance of Syzygium cumini, an important fodder tree, peaked under D-II. Sapkota et al. (2009) also reported the dominance of S. cumini under moderate disturbances. The increased dominance of S. cumini is because of its great seed-setting quality, coping abilities, and evergreen dense canopy (i.e., aggregate dispersion; Table 2), which shades out competition from other species. The total shrub density and BA was lower in D-I, with an average disturbance score of 14.6; D-II, forests with an average disturbance score of 35.0; D-III, forests with an average disturbance score of 57.0; and D-IV, forests with an average disturbance score of 58.2.  

![Figure 5](image-url)  

**Figure 5.** Relationship of tree density (ha) with shrub density (ha). The R² value is the adjusted value. D-I, forests with an average disturbance score of 14.6; D-II, forests with an average disturbance score of 35.0; D-III, forests with an average disturbance score of 57.0; D-IV, forests with an average disturbance score of 58.2.
light-demanding species for regenerating juveniles. Disturbance also increased the dominance of nonpalatable species such as Lantana camara, Ardisia solanacea, and Bombax ceiba. Nonpalatable species percentage was high under heavy disturbance, which suggests that disturbance forces a species composition change toward nonpalatability. In D-III/IV forests, ferns (i.e. scrophylites) were not recorded, which may be because of altered micrometeorological conditions that result from decreased tree cover. Five trees species valued for fodder (e.g. Bauhinia variegata, Bauhinia retusa, Glycyrrhiza glabra, Pterospermum acerifolium, and Pyrus pashia) were not recorded in adult the stage (Table S3).

In general, seedling and sapling density of most species was higher in moderately disturbed forests than in other disturbed forests (Table S4). However, most tree species showed impaired regeneration; the percentage of good and fairly regenerating species decreased with an increase in disturbance (Table 3). Among woody perennials, 31% of species showed good regeneration, 17.2% of species showed fair regeneration, and the remaining species (> 50%) showed poor to very poor regeneration. Terminalia alata and Adina cordifolia were absent in the sapling stage in all forests. However, T. alata existed in the seedling stage with diminished density in all forests, except in moderately disturbed forests. Sapkota et al (2009) attributed this finding to the species’ high light demands. A very high number of seedlings of some species were detected, which declined sharply in the subsequent sapling stage. In the tree layer, except for M. philippinensis and L. monopetala, no other species had a fair accumulation of species in severely disturbed forest (Table S3). In natural settings, this reduction is from resource competition (i.e., space and nutrients) and other biotic factors. In this study, poor regeneration was primarily caused by anthropogenic disturbances. Harvesting (prohibited), cutting and lopping, grazing, and trampling increase light transmittance, which subsequently increases soil temperature and decreases soil moisture. These factors expose seedlings and juveniles to more extreme temperatures at the forest floor level and affect the regeneration of species. Significant differences in soil temperature ($P < 0.0001$) and soil moisture ($P < 0.0001$) were recorded across the DIs (Figure 6).

These results illustrate that moist secondary forests need to be conserved by minimizing the disturbance levels to the lowest possible threshold sensu intermediate disturbance. The emerging forest management paradigm necessitates synergy between community prioritization with sustainable conservation prioritization, and both depend on the health and stability of forests.

This study showed that all parameters of diversity patterns were maximized under moderate disturbance. Any attrition in the composition and structure brought by a cohort of disturbing agents certainly can hamper forest functioning and sustainability and have repercussions on the faunal diversity that inhabit the forests, especially migratory animals, and on interaction reciprocity. Therefore, DIs exceeding intermediate ranges, even in the protected moist tropical forest, may jeopardize its stability for which it has been unmanaged or abandoned.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.japb.2016.01.004.

References


Figure 6. Box and whisker plots (A) soil temperature and (B) soil moisture in different disturbance intensities in Doon Valley forests. Horizontal lines within the boxes indicate the mean values; the upper and lower boundaries of the boxes indicate the standard deviations; and the whiskers span the ranges of individual values measured. Lowercase alphabetical letters indicate the result of post hoc multicomparson Fischer’s least significant difference ($P > 0.05$). D-I, forests with an average disturbance score of 14.6; D-II, forests with an average disturbance score of 35.0; D-III, forests with an average disturbance score of 57.0; D-IV, forests with an average disturbance score of 98.2.


