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Tree community responses to disturbance: Testing the intermediate disturbance hypothesis in different forest management regimes of Nepal

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Abstract

The Intermediate Disturbance Hypothesis (IDH) posits that local species diversity peaks at moderate levels of disturbance. Despite its broad theoretical appeal, empirical validation across ecosystems and disturbance regimes remains limited. This study assesses the IDH in the Terai Sal (*Shorea robusta*) forests of Nepal by examining responses of tree communities to anthropogenic disturbances across three management regimes: buffer zone forests, user group-managed community forests and collaborative forests. The use of the importance value index allowed comparison of stand structure, species composition and diversity indices (alpha diversity measures: Shannon, Simpson, and Margalef indices) and beta diversity (Jaccard similarity). We used redundancy analysis to identify key environmental and disturbance variables that correlated with plant communities. The findings demonstrated significant structural and compositional shifts across the disturbance regimes. While low-disturbance buffer zones are characterised by mature, dominant Sal stands, high-disturbance collaborative forests had an overabundance of seedlings and an absence of mature trees. As predicted by IDH, the most moderately disturbed community forest recorded the highest values of alpha diversity. Beta diversity was pronounced, with each regime having a unique species composition. Community structure was significantly shaped by disturbance intensity, canopy cover and anthropogenic pressures. These results indicate that intermediate levels of disturbance at periodic intervals can sustain tree diversity in the high tropics of the Terai by maintaining a balance in the competition–colonisation trade-offs in a long-term process. Furthermore, managed silviculture practices can enhance diversity by producing heterogeneous conditions in gap settings. The quantitative insights derived from this study could help inform sustainable forest management policies in Nepal, balancing biodiversity conservation with community resource needs. More broadly, the findings underscore the role of disturbance regimes in shaping diversity patterns in tropical production forests and emphasise the necessity of context-specific empirical validation of ecological theories to guide management interventions.

Keywords: intermediate disturbance hypothesis; *Shorea robusta*; community forestry; alpha diversity; beta diversity; Nepal

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Introduction

In a world riven by climate change, biodiversity loss and ever-escalating anthropogenic pressures, understanding the role of disturbances across ecological systems has become critically important. Natural (e.g. windblows, wildfires, and pest infestations) and anthropogenic (e.g. deforestation, urbanisation, and timber harvesting) disturbances act as agents of change that profoundly influence the ecology of communities by altering their structure, composition and functions (Attiwill 1994, Mori 2017). These events generate spatial and temporal variability, increasing biodiversity and allowing ecosystems to adapt to changing circumstances (Seidl et al. 2017, Thom et al. 2018). The Intermediate Disturbance Hypothesis (IDH), propounded by Connell (1978), provides a theoretical framework for understanding these dynamics. The IDH posits that species diversity within a community peak at intermediate levels of disturbance, where disturbances limit the dominance of competitive species, while allowing sensitive taxa to persist, promoting coexistence (Wilkinson 1999, Catford et al. 2012a,b).

In forest ecosystems, disturbance regimes play a pivotal role in creating mosaics of successional patches, shaping community development, species richness and ecosystem dynamics. Research shows that disturbances of varying intensity contribute to biodiversity conservation by maintaining structural and functional heterogeneity (Nagel et al. 2017, Thompson et al. 2021). Moreover, as climate change alters disturbance regimes, understanding these relationships can be integral to developing adaptive management strategies that maintain forest productivity and biodiversity during periods of future uncertainty (Bongers et al. 2009a, Kern et al. 2014a,b, Mori et al. 2021).

In ecological optimism, where shallow forms of ecological systems theory have implausibly strong policy and practical audiences, such as the popular Integrated Ecosystems Management, support for the IDH remains mixed (Mackey and Currie 2001, Fox 2013). Some researchers have observed peak diversity in ecosystems experiencing a certain level of disturbance (Bongers et al. 2009a, 2009b, Kershaw et al. 2017), while others note anomalies in unimodal expectation (Fox 2013, Hayward et al. 2021). The oversimplification of patterns by which one form of disturbance diversifies an ecosystem has been identified as one of the weak points of the IDH, as that pattern may be different for various patches in time and space, ecosystem types and sorts of disturbances (Mackey and Currie 2001, Bongers et al. 2009b). Consequently, there is a pressing need for empirical testing of the IDH across diverse ecological contexts to refine its underlying assumptions and enhance its applicability.

Despite the critiques the IDH has faced over the years, it remains a foundational concept in understanding biodiversity dynamics and is still relevant for several reasons. Firstly, its principles are widely applied in forest management and conservation strategies globally, providing a practical framework for managing biodiversity amidst natural and anthropogenic disturbances (Peterson et al. 1998, Wilkinson 1999). In Nepal and other regions, where community forest management plays a critical role, the IDH allows users to assess the levels of species diversity and ecosystem functioning under varying levels of disturbance.

Secondly, despite extensive theoretical discussions, empirical testing of IDH has been uneven across ecosystems, with limited studies in tropical forests and even fewer in Sal (*Shorea robusta*) forests, which dominate the large parts of South Asia. The humid tropics and subtropics comprise forests with varying disturbance regimes, including rainfall variability, pest outbreaks and anthropogenic activities such as overgrazing and selective logging (Chazdon 2003, Sagar and Singh 2006). Developing the concept of IDH and identifying the best ways to integrate it into such regions is beneficial as a practical tool for understanding the IDH.

The Terai region is characterised by Sal-dominated tropical moist deciduous forests, (as reported by Wikramanayake (2000). These forests contribute to a variety of ecosystem services, including biodiversity conservation, carbon sequestration and livelihood support for local communities (Bhattarai et al. 2021). However, the Terai landscape suffers from extreme fragmentation and degradation as an effect of both exploitation of its resources and unsustainable logging practices (Chaudhary 2000, Paudel et al. 2018). To address these challenges, Nepal has introduced a number of community-driven forest management approaches, including community forests, buffer zone community forests and collaborative forests. Each of these approaches has its own set of institutional frameworks, goals and principles that determine the utilisation of forest products within the regions (Pokharel et al. 2017, Paudel et al. 2018). Generally, these approaches show a range of disturbance intensities. The management regime of the community forest in the buffer zone is more protective in nature and is therefore characterised by a low level of disturbance. Community forests, which permit moderate resource use, correspond to an intermediate level of disturbance. Collaborative forests, involving more intensive utilisation, represent high disturbance. In general, these management regimes provide an ideal setting for investigating the influence of anthropogenic disturbances on tree diversity and test the applicability of the IDH in sustainable forest management. This study applies the IDH framework to Nepalese Terai forests, examining three distinct management regimes that represent a gradient of disturbance intensities.

The primary objective of this study was to assess responses of tree communities to a gradient of disturbances represented by three contrasting forest management regimes in the Nepalese Terai region. Specifically, this research aims to: (1) characterise stand structure and composition across the disturbance gradient, (2) compare alpha and beta diversity patterns among management regimes, and (3) identify key environmental and disturbance variables influencing tree community assembly. We hypothesise that tree diversity will peak at intermediate disturbance levels, aligning with the IDH predictions. Additionally, we expect that the distinct management objectives and silvicultural practices associated with each regime will drive compositional divergence and shape the community structure.

By providing a quantitative assessment of tree community responses to anthropogenic disturbances in a critical biodiversity hotspot, this study contributes to the empirical validation of the IDH, offering insights into the sustainable management of tropical production forests. Our findings can inform forest policy and management interventions that seek to reconcile biodiversity conservation with community resource needs, both in Nepal and in other regions facing similar challenges. Moreover, this work highlights the potential role of disturbance regimes as key drivers of diversity patterns in human-modified ecosystems.

Theoretical framework

Connell (1978) proposed the foundational concept of the IDH, which serves as the theoretical basis for this research. As it stands, this ecological theory remains a cornerstone, as it postulates a moderate rate of disturbance and enriches maximum biodiversity by balancing competitive exclusion and species colonisation. Regardless of the passage of time, in fact, the IDH remains relevant in modern ecological research due to its adaptive nature in various

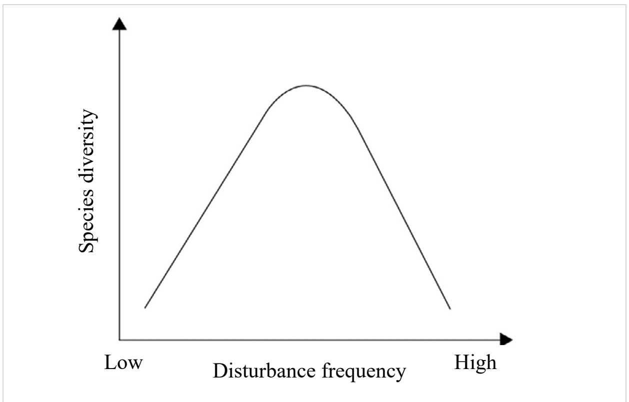

Figure 1. Predicted hump-shaped diversity pattern across the disturbance gradient

contexts (Fox 2013). However, debates regarding its universal application persists, with the emergence of alternative models like the Patch Dynamics Theory (Pickett and White 1985) and the Dynamic Equilibrium Model (Huston 1979) challenging its predictions in certain ecosystems. These assessments underlined the importance of testing the IDH in new patterns to evaluate its explanatory capabilities.

In this study, under community-based forest management practices, the IDH is applied to assess the biodiversity patterns, where disturbances such as selective harvesting and grazing prevail. The IDH model provides a framework for understanding how intermediate disturbances can contribute to biodiversity conservation and ecosystem resilience within a socio-ecological system, and this has proven its relevance within this approach. Hence, by finetuning the IDH in this specific context, this study aims to contribute to the ongoing discourse on the disturbance-biodiversity relationships while addressing gaps in the application of IDH to manage forest landscapes.

Our expectations regarding diversity patterns are defined within the IDH model. Periodic harvesting, for instance, is expected to create a collage of successional stages, preventing the domination of a single species. Consequently, the highest tree species diversity is expected in the moderately disturbed community forest. On the other hand, lower diversity is anticipated in collaborative forests due to species exceeding the tolerance threshold and in buffer zone forests due to competitive exclusion, where both forests are relatively less disturbed.

Materials and methods

Study area

This study was conducted extensively in the Terai region of Nepal, which encompasses a belt of tropical moist deciduous forest (Figure 2) along the southern border with India. The Terai region is characterised by a humid subtropical climate, with average temperatures ranging between 24 and 27°C. This region receives an average annual rainfall of 1,100 to 3,000 mm (DHM 2017). Dominated by Sal (*Shorea robusta*) forests, this region also supports other tree species such as *Terminalia alata*, *Adina cordifolia* and *Lagerstroemia parviflora* (Sapkota 2009).

Quasi-experimental design

A quasi-experimental design was employed to analyse the effects of various forest management regimes on biodiversity and ecosystem resilience. This method involved selecting three diverse forest management systems, where each is implemented within the same region and timeframe. This represents a gradient of anthropogenic disturbance intensity. This management system involved the Bandevi Barandabar Buffer Zone Community Forest (BBBZCF), established in 2001, the Kankali Community Forest (KCF), established in 1995, and the Madhyabindu Collaborative Forest (MCF), established in 2003.

The BBBZCF is located in a buffer zone adjacent to a protected area. Its primary management objective is to

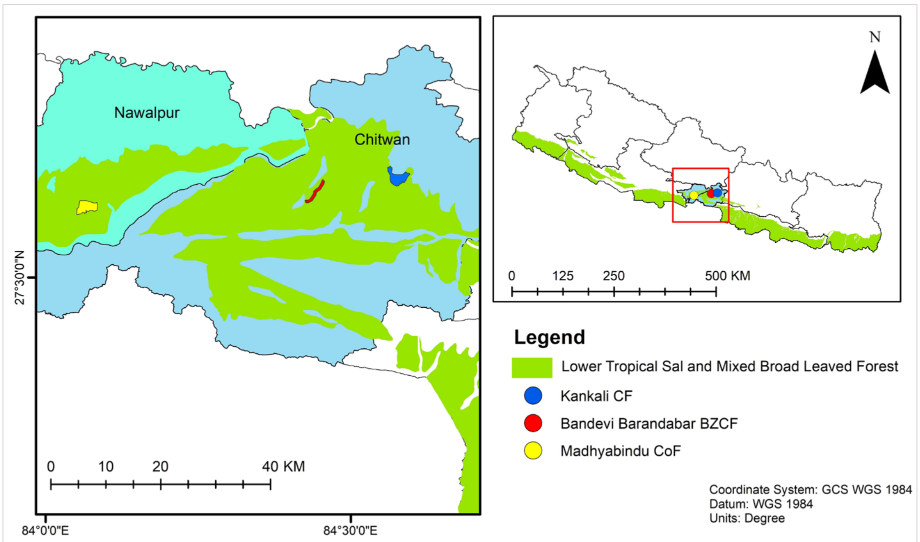

Figure 2. Map of the study area showing the location of the three forest management regimes in the Terai region, Nepal

Table 1. Characteristics of the three forest management regimes studied in the Terai region of Nepal

Characteristics	BZCF	CF	CoF
Objective	Meet the requirements of local people for forest products while preserving biodiversity. (Protection-oriented)	Meet the requirements of local people for forest products while preserving biodiversity. (Conservation-oriented)	Meet the requirement of near or distant users of forest products, revenue generation and active management of forest. (Business-oriented)
Right to sell forest products	Restriction on sale of forest products outside the user group	Community forest user group can sell products outside the user group if there are surplus to local demand	70% of harvest is used by the user group, the remaining 30% by Government of Nepal
Right to manage forest.	BZCF user groups manage and conserve the forest, but the park officials also have authority to engage in conservation	Community forest user group (CFUG) manage and conserve forest according to prescribed management plan prepared by Division Forest Office (DFO)	Collaborative forest user group (CoFUG) and Division Forest Office jointly manage the forest
Intensity of forest harvesting	Low	Medium	High
Management/harvesting practices	Forest users are focused on conservation and silvicultural operations are very limited	Forest users follow management plans and apply regular silvicultural operations like cleaning, thinning, plantation and selective logging almost every year	The user group and DFO follow management plans and apply regular silvicultural operations, such as cleaning, thinning, planting and heavy logging almost every year.

Note: BZCF stands for buffer zone community forest, CF stands for community forest, and CoF stands for collaborative forest.

help the local community in maintaining ecological balance through sustainable forest resource extraction. The management practices in the BBBZCF focus on moderate resource utilisation while ensuring habitat preservation for the wildlife within the buffer zone. The KCF, one of the earliest examples of community forestry in Nepal, follows a sustainable forest product extraction model, emphasising empowerment of the local community and the active involvement of local forest users in management decisions. This regime allows for more intensive silvicultural interventions and harvesting compared to the BBBZCF. In contrast, the MCF is a collaborative forest which operates under a co-management model, involving both government agencies and local communities. Its objectives are to maintain ecological integrity while maximising economic benefits from forest resources. Resource utilisation policies allow for high levels of forest product extraction and an increase in the frequency of silvicultural interventions, resulting in the greatest disturbance intensity amongst the three regimes.

These management regimes were selected for their varying management objectives, institutional structures and resource utilisation practices (Table 1).

The gradient of disturbance intensity they represent – from low in the BBBZCF to moderate in the KCF and high in the MCF – provided a unique opportunity to examine how varying levels of anthropogenic disturbance influence biodiversity and ecosystem resilience. This quasi-experimental framework minimises confounding variables, such as temporal variability, as all three regimes were established within a similar timeframe, and ensures that observed differences are more likely attributable to management practices rather than extrinsic factors.

This design provides a robust basis for testing our hypotheses related to the IDH and assessing the broader implications of both community-based and collaborative forest management practices in the region.

Data collection

To assess the vegetation assessment, a systematic sampling structure was implemented across the three forest management regimes to establish sample plots. Sample plots were correspondingly allocated according to sampling intensity set at 1%, resulting in 161 plots across the sites (46 in the BBBZCF, 56 in the KCF and 59 in the MCF). Each sample plot was a concentric circular layout with a radius of 12.61 m (500 m^2 in area) (Figure 3). Within the parameters of each plot, all tree species were identified and classified into four size classes: seedlings (height < 1.3 m), saplings (height > 1.3 m and diameter at breast height [DBH] < 10 cm), poles (DBH 10–20 cm), and trees (DBH > 20 cm) (Baral et al. 2018). Diameter tape was used to measure DBH and the laser rangefinder was used to measure height.

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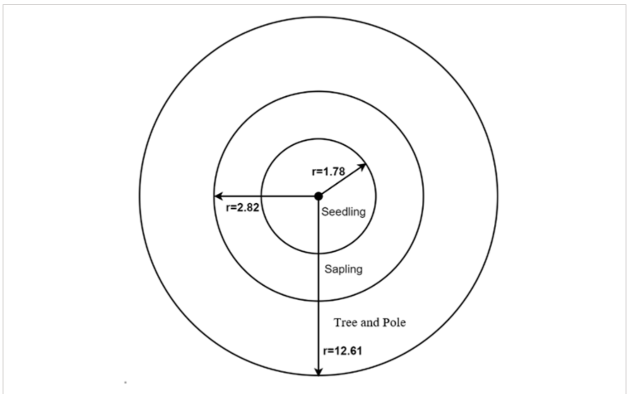

Figure 3. Schematic representation of the concentric circular sample plot design used for vegetation assessment

In addition to vegetation data, variables such as environmental state and disturbances were recorded for each plot, which included canopy cover (%), ground vegetation cover (%), fire damage (%), cattle grazing intensity, wildlife disturbance, cut stumps, and distance from settlements, roads and water sources. The unit for measuring plot distances from settlements, roads and water supplies was the meter. Google Earth's high-resolution satellite imagery and distance measurement tools were used to determine the values. Visual estimations were used to evaluate canopy and ground vegetation covers, whereas evidence of fire damage, cattle grazing and wildlife disturbances was documented based on field observations.

Data analysis

Disturbance analysis

A modified version of the method used by Sagar et al. (2003) was employed to estimate the Disturbance Impact Factor (DIF) for each forest management regime. The DIF was derived from the relative impact of major disturbance sources or indicators.

$$\text{Relative density of damaged individuals (RDD)} = \frac{\sum \text{Number of damaged individuals in all plots}}{\text{Total number of individuals (damaged + normal) in all plots}}$$

$$\text{Relative basal area of damaged individuals (RBA)} = \frac{\sum \text{Basal area of damaged individuals}}{\text{Total basal area (damaged + normal)}}$$

An average of Canopy Cover Percentage (CCP), Number of Occurrences (NOC) of disturbances and average distance of plots from settlement or road for each forest were determined. An impact factor of 1 was assigned to the forest with the lowest RDD, lowest RBA, highest CCP, lowest NOC and highest average distance from settlements or roads. For other forests, relative impact factors were calculated by dividing their values by the corresponding value of the forest with impact factor 1 (or its reciprocal in the case of CCP and distance). The relative impact factors for each forest were summed to obtain the total DIF. Forests were subsequently ranked along a disturbance gradient, ranging from 1 (least disturbed, the lowest DIF) to 3 (most disturbed, the highest DIF).

Diversity indices

Alpha diversity was quantified using three indicators: Shannon diversity index (H'), Simpson's diversity index (D), and Margalef richness index. These indicators were calculated for each sample plot, and an average was taken for each management style. The formulas used for calculating these indices are as follows:

Shannon diversity index (*H*'):

$$H' = -\sum(pi)(\ln pi) ,$$

where pi is the proportion of individuals belonging to the i^{th} species.

Simpson's diversity index (D):

$$\lambda = \sum\left(\frac{n}{N}\right)^2 ,$$

where

n is the number of individuals of a particular species, and

N is the total number of individuals across all species in the community.

$$Margalef\ Index = \frac{(S-1)}{\ln(N)} ,$$

where

S is the number of species, and

N is the total number of individuals.

Beta diversity was assessed using the Jaccard dissimilarity index, which measures the compositional dissimilarity between pairs of sites based on species presence-absence data (Jaccard 1912).

$$J(A,B) = \frac{\text{Number of species shared between } A \text{ and } B}{\text{Total number of species across } A \text{ and } B}$$

Redundancy analysis

Redundancy analysis (RDA) was performed to pinpoint the key environmental and disturbance variables influencing tree community compositions across the three forest management regimes. Before performing the RDA, species abundance data were Hellinger-transformed to account for the presence of double zeros and variations in total abundance among sites. The significance of RDA axes and individual explanatory variables was tested using permutation tests with 999 permutations.

All statistical analyses were conducted in R, version 4.0.3 (R Core Team 2020), using the vegan package for multivariate analyses (Oksanen et al. 2007) and the BiodiversityR Package for diversity calculations (Kindt and Coe 2005, Orwa et al. 2009, Kindt 2025).

Results

Disturbance factor (DF)

Nine disturbance indicators were employed to quantify and compare disturbance levels across the forest management regimes (Table 2). The cumulative disturbance index values revealed notable differences among the regimes, with the MCF experiencing the highest overall disturbance level (sum of indices = 6.63), followed by the KCF, which exhibited an intermediate level of disturbance (sum of indices = 5.42), while the BBBZCF recorded the lowest disturbance (sum of indices = 2.99).

The relative cumulative disturbance index values revealed a gradient.

The quantification of the Disturbance Factor (DF) clearly indicates varying levels of anthropogenic pressure across the three community-based forest management regimes. We observed a gradient of disturbance, with collaborative forests exhibiting the highest intensity of disturbance, followed by community forests and buffer zone forests exhibiting the lowest disturbance levels. These findings align with the expected outcomes based on the legal provisions and management objectives associated with each regime (Table 2).

Table 2. Disturbance indices for the forests at three management regimes

Disturbance index	Management regimes		
	BBBZCF	MCF	KCF
Canopy density	0.84	1.00	0.75
Looping	0.16	1.00	0.26
Litter collection	0.00	0.00	1.00
Forest fire	0.18	0.16	1.00
Encroachment	0.52	1.00	0.00
Pole removal	0.18	1.00	0.49
Tree removal	0.14	0.47	1.00
Damage by wind/storm/hail	0.00	1.00	0.00
Grazing	0.96	1.00	0.93
Total	2.99	6.63	5.42

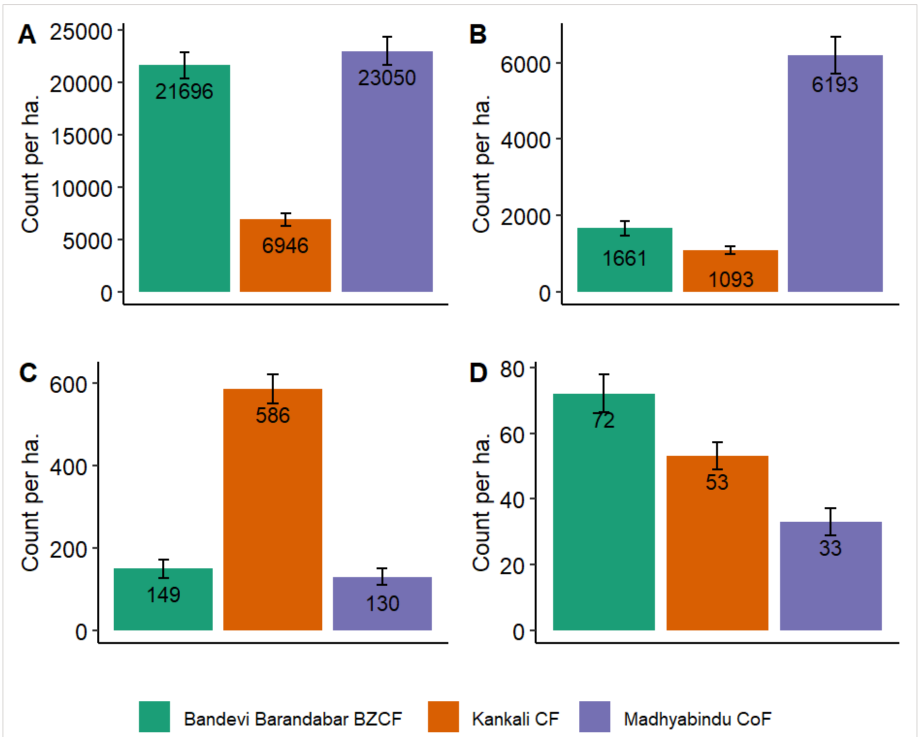

Figure 4. Stand structural characteristics (densities of (A) seedlings, (B) saplings, (C) poles, and (D) trees) at the three forest management regimes

Error bars represent standard errors.

Stand structure and composition

The BBBZCF had the least amount of disturbance, exhibiting the highest density of mature trees (DBH > 20 cm) and basal area. This suggests these areas are relatively undisturbed and well-developed forest stand. In contrast, the MCF forest stand, which experienced the greatest disturbance, had higher densities of seedlings and saplings but a lower density of poles and trees, indicating intensive exploitation of the stands with ongoing regeneration. Meanwhile, the KCF, which has intermediate levels of disturbance, displayed a more balanced size class distribution, with a higher density of poles compared to the forests at other two regimes.

The Importance Value Index (IVI), presented in Figure 5, reveals that Sal is the dominant species across all three management regimes. However, the composition of subdominant species varies among the regimes. In the BBBZCF, *Terminalia alata* and *Adina cordifolia* were identified as the primary associates of Sal; whereas, in the KCF, *Lagerstroemia parviflora* and *Terminalia bellirica* were the most significant subdominant species. By contrast, the MCF was characterised by a higher IVI for pioneer species, namely *Mallotus philippensis* and *Ehretia laevis*, indicating a more disturbed and early successional community structure.

Tree diversity

Species accumulation curves were employed to assess the adequacy of sampling for estimating tree species richness across the three forest management regimes and size classes (seedlings, saplings, poles and trees). Most

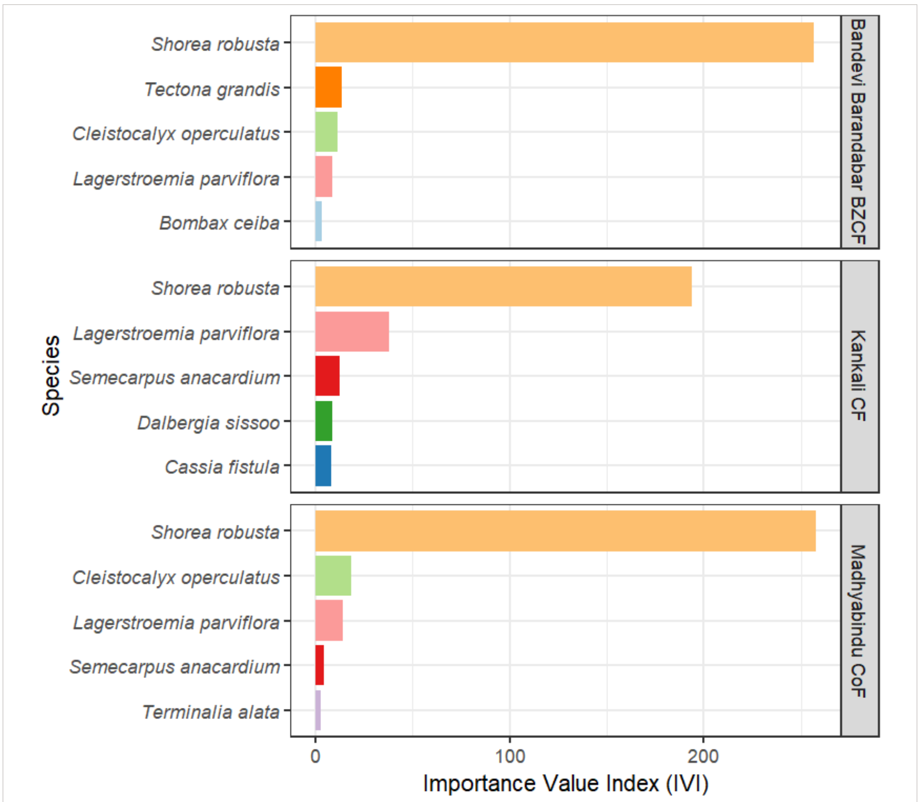

Figure 5. Importance Value Index (IVI) of the top five tree species under each forest management regime

curves tended to asymptote, indicating sufficient sampling to characterise diversity within each forest (Figure 6). However, to comprehensively capture seedling diversity in this system, the steep slope and absence of a plateau in the KCF seedling curve suggest that additional sampling might be required.

A comparison of the species accumulation curve trajectories highlighted differences in species accrual rates amongst the management regimes. The KCF exhibited the steepest curve across all size classes, followed by the MCF with a moderate slope and the BBBZCF with the most gradual accumulation. The curves representing poles and trees tended to reach asymptote more rapidly compared to seedlings and saplings, indicating that the sample size was adequate for the larger size classes (Figure 1).

Across all management regimes, a total of 50 tree species were recorded. It was found that species diversity is the highest in the KCF (36 species), followed by the BBBZCF (17 species) and the MCF (16 species). The mean species diversity per plot was also the highest in the KCF (4.55), with lower values in both the MCF (2.35) and the BBBZCF (2.35) (Figure 7).

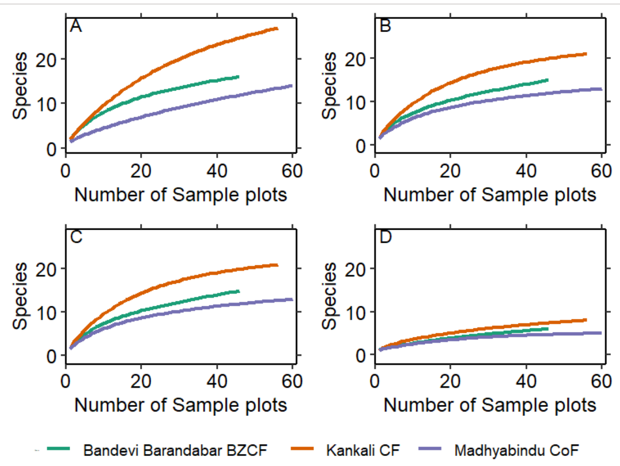

Figure 6. Species accumulation curves for (A) seedlings, (B) saplings, (C) poles and (D) trees in three forest management regimes

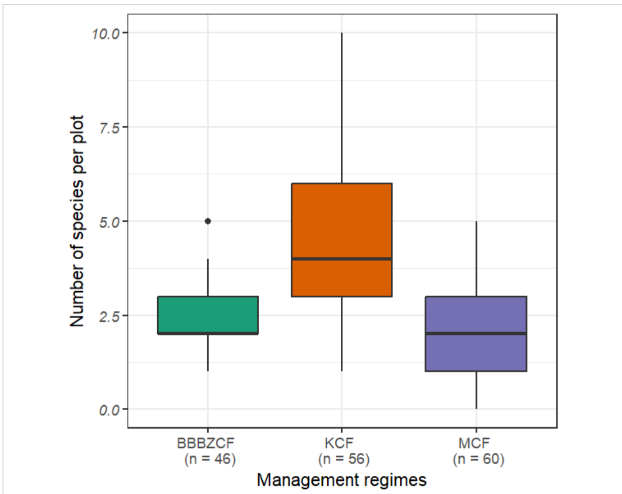

Figure 7. Mean tree species richness per plot under the three forest management regimes

Analysis of variance (ANOVA) showed that management regime had a significant effect on species diversity at the site (F (2, 159) = 41.73, $p < 0.001$). Tukey's Honest Significant Difference (*HSD*) test demonstrated that species diversity per plot was significantly higher in the KCF compared to both the BBBZCF and MCF ($p < 0.001$). No significant difference was observed between the BBBZCF and MCF ($p = 0.9863$).

To further compare tree species diversity under different management regimes, several diversity indices were calculated (Table 3).

To further compare tree species diversity under different management regimes, several diversity indices were calculated (Table 3). Simpson's 1-D index, which measures species evenness, was the highest in the KCF (0.40), followed by the BBBZCF (0.37) and MCF (0.24). Similarly, Shannon's H index, which accounts for the richness and evenness, was the highest in the KCF (1.15), followed by the BBBZCF (0.98) and MCF (0.66). The Margalef index, which assesses species richness relative to the total number of individuals, was also the highest in the KCF (4.53), with lower values in the BBBZCF (2.15) and MCF (1.89). These findings consistently demonstrated that tree species diversity was the greatest in the community-managed forest (KCF), followed by the buffer zone community forest (BBBZCF) and the collaborative forest (MCF).

The Jaccard similarity index values were calculated to compare tree species composition across the management regimes (Table 4). The index values were low (< 0.3) across all pairwise comparisons, suggesting distinct tree species composition under the three regimes. Among the three regimes, the highest similarity was observed between the BBBZCF and the MCF (0.27), which may be attributed by their mature, Sal-dominated forest structures compared to the more disturbed structure of the MCF. However, the low index values still indicated pronounced compositional differences among the sites, with 73–84% of species being unique to the forest stands at each regime.

Table 3. Tree species diversity indices (Simpson's 1-D, Shannon's H, and Margalef) for selected management regimes. *SE* is the standard error

Diversity indices	Bandevi Barandabar BZCF Mean ± *SE*	Kankali CF Mean ± *SE*	Madhyabindu CF Mean ± *SE*
Simpson's 1-D	0.37 ± 0.03	0.40 ± 0.02	0.24 ± 0.02
Shannon's H	0.98 ± 0.08	1.15 ± 0.06	0.66 ± 0.05
Margalef	2.15	4.53	1.89

Table 4. The Jaccard similarity index values comparing tree species composition

Jaccard index	Bandevi Barandabar BZCF	Kankali CF	Madhyabindu CF
Bandevi Barandabar BZCF	1	0.26	0.27
Kankali CF		1	0.16
Madhyabindu CF			1

Environmental and disturbance variables

The redundancy analysis (RDA) identified several significant environmental and disturbance variables shaping species composition in the forest management regimes. It showed that the measured environmental and disturbance variables accounted for 39.5%, 31.14% and 33% of the variation in species composition in the KCF, MCF and BBBZCF, respectively (Figure 8). These proportions are considered reasonably robust for ecological datasets. In KCF, slope, altitude, canopy cover, shrub cover and looping showed significant correlations with diversity patterns

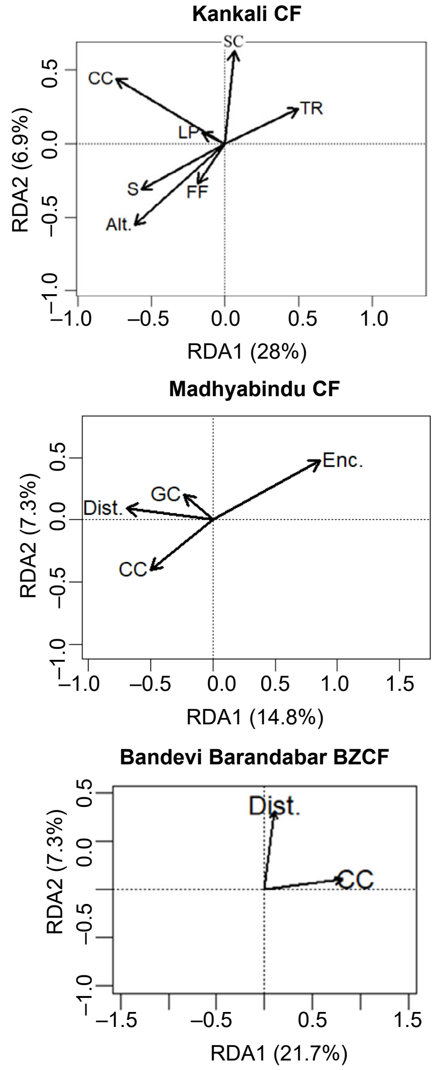

Figure 8. Redundancy analysis showing the distribution of environmental variables in the forest stands under the three management regimes

The environmental variables are abbreviated as follows: altitude (Alt.), canopy cover (CC), distance from settlement/road (Dist.), encroachment (Enc.), forest fire (FF), grass cover (GC), looping (LP), slope (S), shrub cover (SC) and tree removal (TR). Only significant variables in direct selection are presented in the graphs along the RDA axes ($p < 0.05$) (Figure 8). This indicates these factors were influential in determining the tree species composition. The close clustering of these variables suggests they are interrelated in exerting a combined effect on diversity.

In the MCF, canopy cover, grass cover and encroachment demonstrated significant relationships with community ordination along the RDA axes ($p < 0.05$). Among these, encroachment exhibited the strongest correlation with the RDA1 axis, highlighting its critical role in shaping species distributions, potentially by creating light gaps. For the BBBZCF, only canopy cover and distance from settlements/roads were significantly correlated with compositional patterns based on the Monte Carlo permutation tests ($p < 0.05$).

Discussion

Our study revealed a complex relationship between biodiversity and disturbance regime in the management system of the Terai forests in Nepal, confirming the importance of the Intermediate Disturbance Hypothesis (IDH) and highlighting its applicability and implementation across various management regimes. Furthermore, the results support for the intermediate disturbance hypothesis under differing management regimes for the Terai Sal forests in Nepal. Our findings are consistent with studies (Attiwill 1994, Acharya et al. 2011, Mori 2017, Seidl et al. 2017, Astiani et al. 2018, Thom et al. 2018) that disturbances – both natural or anthropogenic – significantly alter the structure, composition, and resilience of communities. This study focused on three forest management regimes, specifically Buffer Zone, Community Forest, and Collaborative Forest, representing different disturbance intensity gradients. It offers a robust basis for testing the IDH predictions.

Tree diversity patterns and the IDH framework

Our analysis reveals that the relationship between disturbance intensity and tree species diversity is unimodal, which supports the predictions by the IDH (Connell 1978, Wilkinson 1999, Catford et al. 2012a,b). The Community Forest in Kinkali (KCF), at intermediate level disturbance (sum of the indices = 5.42), has the highest alpha diversity and species richness (mean = 4.55 species per plot). This result confirms previous studies that disturbances of moderate intensity promote spatial and temporal heterogeneity and, hence, biodiversity by preventing competitive exclusion and allowing coexistence (Chazdon 2003, Maren et al. 2015, Nagel et al. 2017, Thompson et al. 2021). The structural and compositional heterogeneity observed in the Community Forest exhibits similar findings of mixed-severity disturbance studies (Bongers et al. 2009a, Kern et al. 2014a,b, Mori et al. 2021).

On the other hand, the BBBZCF has significantly lower levels of disturbance, which may promote competitive exclusion under such low-disturbance conditions. Similarly, several early studies have also noted on the IDH (Mackey and Currie 2001, Molino and Sabatier 2001, Fox 2013). In contrast, the MCF was less diverse (mean = 2.35) due to more intense resource extraction and higher disturbance intensity (sum of indices = 6.63). Such a pattern corresponds to the general observation of tropical and subtropical forest systems, where high-intensity disturbance generally leads to reduced diversity (Chazdon 2003, Sagar and Singh 2006, Nugroho et al. 2022a).

Management regimes and ecosystem resilience

We observed differences in community structure and composition, which were partly related to the different management objectives and silvicultural practices between the three regimes. The management approach in the Buffer Zone Forest promotes biodiversity conservation; however, this approach may also reduce the potential for recruitment of disturbance-dependent species (Peterson et al. 1998, Wilkinson 1999, Puettmann et al. 2009). Moderate utilisation in the Community Forest maintains a balance between biodiversity conservation and sustainable resource use, which also follows similar conclusions from other community-based forest management systems (Shrestha et al. 2013a, Pokharel et al. 2017, Paudel et al. 2018). However, overexploitation and habitat fragmentation have rendered the communal forests unable to support biodiversity, which again coincides with the concerns raised by Paudel et al. (2018) and Chaudhary (2000).

Environmental and disturbance variables

The RDA showed that, in the environmental and disturbance variable sets, 39.5%, 31.14%, and 33% variation in species composition was accounted for in the KCF, MCF, and BBBZCF, respectively. Therefore, important variables such as canopy cover, encroachment, looping, and grazing were found to be significantly associated with the diversity patterns ($p < 0.05$). For example, in the MCF, the strong correlation of encroachment with species distributions suggests its role in determining light gaps and regeneration (Figure 8). These findings parallel studies that have demonstrated the importance of microhabitat variability for maintaining diverse assemblages (Bongers et al. 2009b, Sapkota et al. 2009, Kershaw et al. 2017).

Tree species composition and diversity indices

Species richness was significantly different among the forests with the three different management regimes ($p < 0.001$). The management regime in the KCF presented the highest richness, with 36 species, followed by the BBBZCF and MCF, with 17 and 16 species, respectively.

Diversity indices follow the same trend: Simpson's index is 0.40, Shannon's index is 1.15, and Margalef's index is 4.53 for the KCF. Such marked diversity in the KCF agrees with the IDH model, according to which disturbance at the intermediate levels would favour richness and evenness (Connell 1978, Mackey and Currie 2001, Catford et al. 2012a,b).

The Jaccard similarity indices (< 0.3) indicated distinct species composition among regimes, with the highest similarity between the BBBZCF and MCF (0.27). The distinction between these sites implies localised adaptation and differential species turnover, further supporting the role of disturbance gradients (Table 4).

Policy implications and forest management

The results of this study have important implications for the sustainable management of tropical forests, and particularly the Terai Sal forests in Nepal. The IDH provides a conceptual framework for developing silvicultural systems that promote high tree diversity while facilitating the availability of forest goods and services (Puettmann et al. 2009). These results suggest that moderate disturbance regimes, like those in the community forestry model, may favour coexistence and promote diversity. Similarly, moderate harvesting regimes in the Community Forests may provide models that enhance ecosystem resilience under climate change, while avoiding over-exploitation in Collaborative Forests and improving opportunities for recruitment in the Buffer Zone Forests can further optimise biodiversity outcomes (Holling and Meffe 1996, Bongers et al. 2009a, Kern et al. 2014a,b, Mori et al. 2021).

Forestry professionals can use the results obtained to develop management strategies that create a mosaic of disturbed areas and growth stages within a forest, mimicking the natural disturbance patterns that historically supported biodiversity in these ecosystems (Puettmann et al. 2009). At the same time, however, efforts toward minimising fragmentation should be emphasised to ensure the maintenance of ecosystem functions and biodiversity (Astiani et al. 2018).

It is therefore appropriate to acknowledge the complexity of the diversity-disturbance relationship (Mackey and Currie 2001, Miller et al. 2011). The disturbance regime that best maintains diversity might be ecosystem-, management objective-, and/or society/community-dependent (Kershaw and Mallik 2013). Moreover, long-term impacts of disturbances on the resilience and functional integrity of ecosystems are not accounted for by the IDH (Holling and Meffe 1996, Hughes et al. 2007).

Conclusion

It thereby evidences the IDH for the Terai Sal forests in Nepal under different management regimes. The highest tree species diversity in moderately disturbed community forests is also acceptable within the IDH predictions. The significant variability in stand structure and composition along the disturbance gradient caused by the three management regimes highlights the complex interactions between disturbance levels and practices for managing forest ecosystem characteristics. These results further highlight two main approaches to sustainable forest management: adaptive management strategies, which consider ecological and socio-economic factors. In the future, long-term monitoring of different management regimes is needed to fully understand the impact of a given regime on forest dynamics and ecosystem services over a given period. This will be crucial in developing a management approach that responds to the constantly changing ecological and social conditions within Nepalese highly varied forest landscapes.

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