Tree Regeneration Characteristics in Limestone Forests of the Cat Ba National Park, Vietnam

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Research article

Keywords: regeneration, environmental factors, national park, species richness, overstory-regeneration ratio

DOI: https://doi.org/10.21203/rs.3.rs-244706/v1

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Abstract

Background: Forest regeneration is decisive for future forest development and therefore of major concern to forest ecologists. The ability of overstory tree species to regenerate successfully is important for the preservation of tree species diversity and its associated flora and fauna. This study investigated forest regeneration dynamics in the Cat Ba National Park, a biodiversity hotspot in Vietnam. Data was collected from 90 sample plots and 450 sub-sample plots in the regional limestone forests. We compared species richness between the regeneration and overstory tree layers and examined the effect of environmental factors on the occurrence of regeneration. We developed five ratios to relate overstory and regeneration richness and diversity.

Results: We found 97 tree species in the regeneration layer compared to 136 species in the overstory layer. Average regeneration density was 3,764 ± 1,601 per ha. Around 70% of the overstory tree species generated offspring. Of the tree species threatened according to The International Union for Conservation of Nature’s Red List of Threatened Species, only 36% were found in the regeneration layer. A principal component analysis provided evidence that the regeneration of tree species was linked to terrain factors (percentage of rock surface, slope) and soil properties (Cation exchange capacity, pH, humus content, soil moisture, soil depth). Contrary to our expectations, the prevailing light conditions (total site factor, gap fraction, openness, indirect site factor, direct site factor) had no influence on regeneration density and composition, probably due to the small gradient in light availability.

Conclusion: We conclude that tree species richness in Cat Ba National Park appears to be declining at present. We suggest similar investigations in other biodiversity hotspots to learn whether the observed trend is a global phenomenon. In any case, a conservation strategy for the threatened tree species in the Cat Ba National Park needs to be developed if tree species diversity is to be maintained.

Background

Forest regeneration plays a key role in forest development. In managed forests, it ensures the survival of tree species after the overstory layer has been harvested. In natural forests it is key to the resilience of an ecosystem after natural disturbances [1–6]. Thus, forest regeneration status determines the future of a forest ecosystem [4]. However, the regeneration layer also directly depends on the structure of the standing tree layer [2, 7, 8] and reflects forest resilience and vitality [3, 9, 10]. When a forest ecosystem lacks sufficient natural regeneration of certain tree species, tree species diversity is lost, which may in turn affect related ecosystem functions and services in the long term [4, 9, 11–13]. Therefore, research on natural forest regeneration dynamics and on potential factors influencing successful regeneration will increase the understanding of long-term functioning and stability of forest ecosystems [14].

Studies of the impacts of abiotic and biotic factors on establishment, survival, and increase in natural regeneration have been conducted worldwide in different forest types [1, 3, 4, 6, 15–24]. Research on regeneration patterns in tropical forests is, however, still scarce (but see below). Nevertheless, this
research is critical due to the contributions of tropical forests to global biodiversity [25–28]. Southeast Asia harbors approximately 15% of the world's tropical forests [29] located in countries such as Cambodia, Indonesia, Malaysia, Myanmar, the Philippines, Thailand and Vietnam. This part of the world can be regarded as a biodiversity hotspot where the greatest number of endemic and threatened species in the world can presumably be found [26, 30]. It is, therefore, highly important for biodiversity conservation. In addition, these forests are important for environmental protection, socio-economics, and the living conditions of forest-dependent populations [31]. However, to maintain these tropical forests and their diversity, we need to understand the degree to which tree regeneration patterns depend on abiotic and biotic factors and how they change due to natural or human disturbances [32]. Many studies have examined tree diversity of saplings in dependence of light and water availability in tropical forests, and on the regeneration patterns within gap-understory habitats in tropical rainforest environments [26–30, 33–35]. Research on natural regeneration under potential limiting factors other than light are rare, however, especially in Southeast Asia.

In 1943, 14.3 million hectares of natural forests could be found in Vietnam, accounting for 43% coverage of its total land area [36, 37]. In the period from 1943 to 1990, the quality and quantity of forests had severely declined due to multiple socio-economic factors, unsustainable management, and consumption. The forests in Vietnam reached their lowest coverage (27%) in 1990 [36–38]. Due to government policy, forest cover increased to 42% in 2019 [39]. This was achieved both by protecting the remaining natural forest ecosystems, and by establishing five million ha forest plantations [39]. These measures reduced the pressure on forests such that forest area increased to 13.8 million ha in 2019 [36, 38, 40]. At the same time, the Vietnamese government also established protected areas and national parks across the country to enable recovery of secondary forests and to protect primary forest ecosystems [36, 41]. So far, 30 national parks and protected areas have been established in Vietnam [41, 42]. Due to past unsustainable management practices, most natural forests in Vietnam now are secondary forests; primary forests are restricted to core zones of protected areas or national parks [36]. To date, few studies have focused on forest regeneration in these forests. Dao and Hölscher [43] examined the regeneration status of three threatened species in north-western Vietnam, and found that most of those tree species regenerated in core zones while their regeneration was poorer in buffer zones and restoration zones. Van and Cochard [44] suggested that forest isolation contributed to decreasing regeneration of rare tree species in lowland hillside rainforests in central Vietnam. Blanc, et al. [45] conducted a study on forest structure, natural regeneration status and floristic composition at five locations in Vietnamese Cat Tien National Park. Their results showed that tree species diversity in the regeneration layer decreased due to the dense canopies of the dominant tree species. Tran, et al. [46] studied the regeneration of 18 commercially valuable tree species after 30 years of selective logging in Kon Ha Nung Experimental Forest, Vietnam. Their results indicated that tree regeneration density in intensively managed forests was significantly higher than in low impact and unlogged forests. However, to our knowledge, no study has yet addressed natural forest regeneration in the limestone forests of Vietnam, even though they are diversity hotspots and habitat for many threatened tree species [47].
The regeneration layer is known to be influenced by overstory composition [48, 49], abiotic factors [9, 50], and biotic factors [4]. Here we investigated natural forest regeneration in Cat Ba National Park (CBNP), located on limestone islands in Vietnam [51–53]. Specifically, we sought to identify the impact of environmental factors on natural regeneration diversity by focusing on two main questions: (1) Does tree species richness in the regeneration layer resemble the tree species richness in the overstory, indicating a high stability in tree species richness? (2) If species richness differs among the different layers, which environmental factors drive the species richness gap between the overstory and the regeneration layer?

Results

Overstory - Regeneration species richness status

In the 90 sample plots, we found a total of 97 tree species in the regeneration layer (Appendix E) compared to 136 species in the overstory tree layer (Appendix D), indicating that species richness in the overstory layer was higher in almost every sample plot compared to the regeneration layer (Fig. 1). We observed a similar pattern for the threatened tree species (Fig. 2). The average density of regeneration trees was 3,674.42 ± 1,601.62 ha⁻¹ (mean ± sd).

Results of the extrapolation approach showed that sample size (m, number of individuals) and coverage-based estimates of tree species diversity in the overstory and regeneration layers clearly differed for the whole study area across the three investigated Hill numbers (Fig. 3, see Appendix D, Appendix E). In the overstory layer, there were 136 species belonging to 2301 observed individuals, with an estimated completeness of sample coverage of 99.2%. Extrapolating to a sample coverage completeness of 100% increased species richness to 143 species belonging to 8000 individuals. In the regeneration layer, there were 97 species belonging to 3622 individuals with an estimated completeness of sample coverage of 99.8% (Fig. 3, see Appendix D, Appendix E). Extrapolating to a sample coverage completeness of 100% increased species richness to 100 species and 8000 individuals (Fig. 3, see Appendix D, Appendix E). The estimated diversity ratios of overstory and regeneration layers were 0.71 for interpolation based on observed values, and 0.70 for extrapolation, respectively.

Neither specific environmental factors (Table 1) nor the first three principal components (Table 2) were significantly correlated with tree regeneration density in the linear mixed effect models.
Table 1
Linear mixed effect model results of tree regeneration density and six environmental factors which were most strongly correlated with first three PCs (see more Appendix G). Acronyms of variables are defined in Table 5. Value column is the coefficient value of variables; t-value, t-test for coefficient value, p-value of hypothesis test (p-value < 0.05).

| Variables | Value   | Standard Error | df | t-value | p-value |
|-----------|---------|----------------|----|---------|---------|
| Intercept | 3819.32 | 992.92         | 81 | 3.847   | < 0.001 |
| L_TSF     | -21.48  | 64.85          | 81 | -0.331  | 0.741   |
| L_GF      | -3.73   | 46.41          | 81 | -0.080  | 0.936   |
| S_CEC     | -38.19  | 106.73         | 81 | -0.358  | 0.721   |
| T_RS      | -9.02   | 5.68           | 81 | -1.587  | 0.116   |
| S_clay    | -20.11  | 15.63          | 81 | -1.286  | 0.202   |
| S_silt    | 25.63   | 16.11          | 81 | 1.591   | 0.115   |

Table 2
Linear mixed effect model results of tree regeneration density and the first three principal components. Value column is the coefficient value, t-value t-test for coefficient value, p-value of hypothesis test (p-value < 0.05).

| Variables     | Value   | Standard Error | df | t-value | p-value |
|---------------|---------|----------------|----|---------|---------|
| Intercept     | 3220.53 | 363.098        | 80 | 8.870   | < 0.001 |
| PC1           | -88.09  | 54.555         | 80 | -1.615  | 0.110   |
| PC2           | -127.70 | 71.060         | 80 | -1.797  | 0.076   |
| PC3           | -75.87  | 81.576         | 80 | -0.930  | 0.355   |
| PC1:PC2       | 10.77   | 32.874         | 80 | 0.328   | 0.744   |
| PC1:PC3       | -79.89  | 41.627         | 80 | -1.919  | 0.058   |
| PC2:PC3       | 7.55    | 42.768         | 80 | 0.177   | 0.860   |
| PC1:PC2:PC3   | -0.90   | 21.475         | 80 | -0.042  | 0.966   |

Overstory - Regeneration ratios characteristics

The five ratios clearly indicate that the regeneration layer does not reach the diversity level of the mature tree layer because all five ratios fell below 1 on average (Fig. 4). This result was also confirmed by the one sample t-test, with all five ratios being significantly lower than 1 (Table 3). Separated into the height classes, the true diversity and species richness ratio were smallest for the height class < 50 cm (0.2 and 0.17, respectively) and highest for the height class considering regeneration > 200 cm < DBH 5 cm (0.46 and 0.42, respectively) (see Appendix F). Results also show that the regeneration layer only reaches 70 %
of the diversity of the overstory layer, with only 38% of the overstory tree species regenerating successfully within a sample plot (Table 3). Interestingly, 30% of the regenerating tree species came from mother tree species presumably located outside the sample plots, as they were not present in the overstory (Table 3). Offspring were found for only 36% of the mature threatened tree species (Table 3).

Table 3
One sample t-test results for the five calculated ratios relating species richness of the regeneration and the overstory layers. Shown are mean values (Mean) and estimated confidence intervals (Confident interval) as well as t-values, degrees of freedom (df) and p-values. Significance is assigned at p < 0.05.

| Ratio                        | Mean  | Confident interval (95%) | t-value | df  | p.value |
|------------------------------|-------|--------------------------|---------|-----|---------|
| Species richness ratio      | 0.68  | 0.59–0.77                | -7.06   | 89  | < 0.001 |
| True diversity ratio        | 0.69  | 0.60–0.79                | -6.48   | 89  | < 0.001 |
| Same species ratio          | 0.38  | 0.35–0.42                | -33.49  | 89  | < 0.001 |
| New existent species ratio  | 0.30  | 0.20–0.39                | -15.02  | 89  | < 0.001 |
| Threatened species ratio    | 0.36  | 0.26–0.46                | -12.37  | 89  | < 0.001 |

Principal components as independent environmental gradients.

The first three principal components (PC) of the PCA explained 54.14% of the variation in environmental characteristics among plots. PC1 (23.5% explained) had the highest loadings for different light availability factors, while PC2 (19.7%) represents soil fertility (CEC, humus content), percentage of rock surface, soil moisture, soil depth, and pH. PC3 (10.9%) represents the soil texture (silt, clay, and sand) (see Appendix G, Fig. 5).

The vectors of the different light variables (L_DSF, L_TSF, L_ISF, L_GF, L_OPN) were strongly positively correlated. They were all strongly associated with PC1 and hence this is what PC1 shows: light (Fig. 5).

Similarly, soil properties (S_CEC, S_pH, S_SH, S_SM, S_BS), and terrain factors (T_RS, T_SI) were positively correlated to each other and with PC2 (Fig. 5). Otherwise, soil depth (S_SD) and soil acidity (S_HA) were negatively correlated with PC2 (Fig. 5).

Linear mixed effect models between ratios and PCA axes and environmental factors

For three out of five ratios, PC2, which combines a gradient of fertility (S_CEC, S_SH), percentage of rock surface, and moisture, was the best predictor (Table 4). Thereby, an increasing PC2 axis values slightly reduced species richness ratio (SRR), true diversity ratio (TDR), and new species ratio (NSR), indicating that the difference between the forest layers increases with soil fertility, soil moisture, and rock surface. The percentage of rock surface best predicted the same species ratio. An increasing percentage of rock surface reduced the same species ratio, indicating that only certain tree species were able to regenerate...
on rough terrain (Table 4). Light variables, summarized as PC1, were the best predictors for the threatened species ratio, but with no significance (Table 4). In general, marginal and conditional $R^2$ values were very low, showing that the recorded environmental variables could explain only a small proportion of the variation.

### Table 4

Summary of best-fit models. Slope values are given in parentheses. logLik, log-likelihood estimation; AICc, Akaike information criterion; p-value, significant value below 0.05; marginal $R^2$, variance explained by fixed effects; conditional $R^2$, variance explained by both fixed and random effects.

| Ratios            | Intercept | Predictor variable | logLik | AICc | p_value | Marginal $R^2$ | Conditional $R^2$ |
|-------------------|-----------|--------------------|--------|------|---------|----------------|------------------|
| Species richness  | 0.683     | PC2 (-0.052)       | -52.750 | 114.0 | 0.02    | 0.068          | 0.094            |
| True diversity    | 0.699     | PC2 (-0.048)       | -56.344 | 121.2 | 0.04    | 0.053          | 0.097            |
| Same species      | 0.494     | Rock surface (-0.002) | 31.970  | -55.5 | 0.00    | 0.092          | 0.541            |
| Newly occurred species | 0.297   | PC2 (-0.061)       | -55.019 | 118.5 | 0.00    | 0.090          | 0.090            |
| Threatened species | 0.359    | PC1 (-0.026)       | -67.496 | 143.5 | 0.23    | 0.016          | 0.016            |

### Discussion

Seedling density in the regeneration layer is an important property for successful regeneration. Our results demonstrate that the average regeneration density of CBNP was 3,674 ± 1,602 trees per ha (see results section). This mean density is considerably higher than that of sub-tropical forests [4], but comparable with other forest locations in Vietnam, such as the Highlands forest (around 3400 tree per ha) [46] and limestone forests in Quangninh Province, Vietnam (3814 tree per ha) [54]. However, in Vietnam even higher regeneration densities have been reported. For example, in the Cat Tien National Park, tree regeneration density ranges from 2850 to 8150 trees per ha [45]; in other broadleaf evergreen forests of Vietnam (Xuan Son National Park) densities reaching around 35000 trees per ha have even been reported [55]. Since we could not identify any specific environmental factor explaining variation in regeneration density, we can only speculate about the most important drivers. It is known from studies in various biomes around the world that light availability plays a crucial role in regeneration abundance and distribution [3, 6, 56]. It is likely that the narrow range of light availability (from 8.21 (± 2.75) to 10.37 (± 11.68), e.g. for ISF see Table 5) in our study prevented us from confirming its importance in our case.
However, even if significant differences in light availability only partially explain regeneration density [56], it is known from other studies that disturbances due to logging [46], livestock browsing, and microsite characteristics [17] are additional explanatory factors in seedling density variation. However, in our study, environmental factors and human disturbances did not appear to affect tree regeneration density (Table 1, Table 2). Our results suggest that competition within the regeneration layer may also play a role, indicating the importance of dominant tree species [57]. Thus, the eight most dominant tree species in the regeneration layer accounted for 54% of all seedlings and the 16 most dominant tree species, representing 72% of total seedling abundance (see Appendix A). Our inconclusive results underscore the need for additional research to explain regeneration density more mechanistically. Approaches should focus more on species traits, such as how fruit coat requires specific environmental conditions to allow successful germination and establishment [58].

Many studies have used seedling, sapling, and mature tree species densities as criteria for forest regeneration evaluation status [4, 7, 59]. Forests are classified as having good regeneration potential when number of seedlings > number of saplings > number of trees; the potential is poor if the numbers of seedlings and saplings are fewer than the present mature tree species [4, 7, 59]. We question the suitability of this approach for some forest types since it does not take developmental stages into account; for example, where mature tree density is so high that regeneration is inhibited due to low light availability. These forests should not rate as poor since their potential for regeneration may still be high. We modified this approach, focusing on species richness and diversity indices of the tree regeneration and overstory layer rather than on tree density. Even though this approach is also quite simplistic and may not consider different recruitment events over time that may have shaped the regeneration as well as the overstory [60], relating overstory and regeneration richness and diversity can give insights to potential trajectories of tree species richness. We found that tree species richness and diversity in the regeneration layer was lower than in the overstory layer (see Fig. 1, Fig. 2, Fig. 3). The 97 tree species that were found in the regeneration layer accounted for 71% of the overstory tree species (136 tree species) (see results section, Appendix D, Appendix E). After extrapolation for completeness of sample coverage, species richness in the overstory was 1.43 times higher than species richness in the regeneration layer (see results section, Fig. 3). Our results are comparable to the other studies conducted in Vietnam. Tran, et al. [46] found 107 tree species in the sapling stratum and 90 tree species in the seedling stratum compared to 144 tree species in the overstory layer in an evergreen broadleaf forest. Blanc, et al. [45] reported tree species numbers of 92, 83, 53, 1, and 43 respectively in five one ha sample plots in the overstory layer of Cat Tien National Park, whereas the number of regeneration tree species were 50, 52, 20, 1, 24, respectively.

The found poor status of species richness in the regeneration layer in our study was verified by the various ratios (Fig. 4, Table 3). In addition, separating the regeneration into height classes indicates that the gap between overstory and regeneration richness and diversity is even increasing with time, as the ratios were highest for the largest height class representing the oldest regeneration (Appendix F). Our results may therefore hint towards potential community alterations in the future that have been observed in other tropical forests [61, 62]. Decreasing species dispersal by large vertebrates is mentioned as an
important factor for such community alterations [61]. In our study, only 38% of the regenerating tree species came from overstory tree species (same species ratio), 30% came from outside the plots (newly occurring species ratio) (Table 3). The trend was also observed for the threatened tree species, which had an equally poor regeneration species rate (36%) (Fig. 2, Table 3). Interestingly, the threatened tree species were mainly found around the parent trees in our study area. According to Janzen [63], seed density of a given tree species decreases with distance from the parent tree but also varies with seed size and seed dispersal processes, and is affected by plant parasites and seed-eating animals. However, more detailed research is needed to determine whether low seed production, low germination rates, low survival rates or insufficient dispersal can explain the observed low representation of mature tree richness in the regeneration layer.

Many previous studies have found that a single environmental factor fails to explain forest regeneration characteristics [1, 3, 4, 6, 7, 9, 11, 15–17, 19, 24, 50, 57, 64–68]. These results are confirmed by our study, since we found that PC2, which represented a fertility, rough terrain, and moisture gradient (see Appendix G, Table 4, Fig. 5), explained the pattern of tree species regeneration better than single environmental variables. However, the marginal R^2 values of each model (Table 4) were very small, so although we can confirm a link between species richness ratios and environmental factors, we did not observe a strong relationship. We assume that other unidentified factors or factors functioning on a larger scale must be considered such as rainfall seasonality [69], water erosion [70, 71], and flooding period [72, 73]. In particular, increasing extreme events can have major impacts on seedling establishment effective over extensive areas. In general, tropical forests are considered as very sensitive to changing climatic conditions and interannual climate variability as the forests display for example strong coevolutionary interactions and specializations that can be decoupled by global change. In addition, changing environmental conditions may eliminate the narrow niches in tropical forests and by this species diversity [74, 75].

As previously mentioned, one important factor affecting tree regeneration patterns at the local scale may be light availability. However, we did not find an influence of light-related factors (represented by PC1) on the tree species richness and diversity ratios (Table 4); we assume that our gradient in light availability was too small (Table 5). Therefore, we can only speculate as to whether higher light availability would have resulted in more balanced ratios between overstory and regeneration tree species richness.

Previous studies have also demonstrated variability in tree species composition along topographic gradients [18, 76–82], because topography affects soil formation (including soil fertility, moisture, and depth) and creates microhabitats [80, 81, 83, 84]. Microhabitats contribute to regeneration niches which in turn are strongly linked to species coexistence [23, 65]. In our research, topography was represented by the percentage of rock surface, slope, and elevation. We assume that a combination of rock surface, slope, and limestone ridges strongly affect soil characteristics (soil nutrient status, humus, soil moisture, and depth), which may have implications for seed storage ability [6, 59]. With increasing percentage of rock surface, soil cover and soil depth decrease (Table 4, Fig. 5, Appendix G). Furthermore, with increasing slope, soils become shallower, store fewer nutrients, and are more prone to erosion. Therefore, factors
indicating rough terrain may have created unfavorable conditions for seed storage and germination [6, 80].

Besides topography and light, soil factors are considered as most important for natural forest regeneration [2, 3, 16, 17, 65, 67, 77, 85]. In our study, soil moisture as well as base saturation and CEC were represented by PC2 and affected the species richness ratios negatively. However, this unexpected result may be a methodological artifact, since soil moisture and soil chemical properties were determined for the upper 20 cm of the soil only. It is likely that these 20 cm do not sufficiently represent the real status of soil moisture and soil fertility. This view is supported by the finding that soil depth was negatively correlated to PC2, and thus influenced the species richness ratio positively.

Forest regeneration of tree species depends on both natural disturbances and anthropogenic activities. Natural disturbances can increase the variability in light conditions, influence seed arrival, and contribute to the diversity of seeds by providing regeneration niches [23, 86, 87]. In addition, natural disturbances also affect recruitment patterns of colonizing species, influence soil resource levels, and determine longer term community development [88]. Human activities may have similar effects but they can additionally affect seed bank composition, for example by removing dominant tree species [67, 88]. However, we did not find a strong effect of human disturbances on species richness and diversity ratios. Only the number of footpaths was related to PC2 (r=-0.21) (see Appendix G, Fig. 5). But this relationship was negative; therefore, the number of footpaths had a positive effect on the ratios, lending support to the idea that disturbances can promote the regeneration process. This is supported by Tran, et al. [46] who found a higher similarity between the regeneration and overstorey richness in forests with high intensity selective logging compared to forests with a lower management intensity or unlogged forests after 30 years because of sufficient sunlight reaching the forest floor to facilitate seed germination and seedling growth. Although we do not have records of natural disturbances or historic human impact, long-term effects of former disturbances may still be reflected in the richness and composition of the regeneration layer or even more so of the overstorey layer and can explain current richness differences between layers [60, 89, 90]. Thus, both natural disturbance and historical human influence should be taken into account when investigating regeneration patterns of tree species including threatened species.

**Conclusions**

Our results indicate that a considerable number of tree species that can be found in the overstory of the forests in the CBNP is absent in the regeneration layer. We interpret this finding as an indication that tree species diversity appears to be decreasing. Since we were not able to explain the resulting pattern to a satisfying degree even though a large number of potentially influencing variables were tested, unidentified factors such as species dispersal or factors functioning on a larger spatial scale may be decisive. Thus, future research may make use of experiments to learn more about the autecology of the different tree species or to examine the impact of climate change on regeneration processes. Also evaluating the impact of natural forest recovery after historical (natural or human) disturbances should be observed in detail as different time scales may have shaped the tree layers.
Building on our results and with additional knowledge, conservation strategies could be developed for maintaining tree species biodiversity. Since we only recorded regeneration status at one point in time, we suggest continuous monitoring of its development by using the ratios introduced here. This would make it possible to address the question of species turnover and diversity change with more certainty for the Cat Ba National Park.

**Methods**

**Study Site**

The data presented stems from northern Vietnam and was collected in the CBNP (20°44′ to 20°55′ N, 106°54′ to 107°10′ E). The national park is part of the Cat Ba Island archipelago located in the South China Sea. CBNP lies to the South of Halong City (25 km), and the Capital Hanoi is found 150 km northwest to CBNP (comp. Figure 6).

CBNP is comprised of 366 islands of varying size [51, 91]. The main rock bed is limestone. The park has a total size of nearly 16,200 ha. This includes maritime (5,265 ha) and terrestrial sites (10,932 ha) [51, 52]. The highest point of the park lies at 331 m above sea level, whereas the average elevation lies around 125 m above sea level. CBNP has a heterogeneous topography with slopes ranging from 15° to 35° [53]. The climate of CBNP is humid sub-tropical with precipitation sums of around 1500–2000 mm yr$^{-1}$, an average humidity far above 80%, and an average temperature of 23°C yr$^{-1}$. The rain season lasts from May through October and the dry season lasts from November to April [51, 92].

The forest ecosystems of CBNP are diverse and include evergreen limestone forests, wetland high mountain forests, and mangroves, next to caves and maritime coral reefs [51, 92]. The evergreen broadleaf tropical rain forests of CBNP can be categorized as undisturbed primary forests or secondary forests, which have undergone significant disturbances through humans [93]. The secondary forests are mainly in the lower parts of the park and in the limestone mountains. Other secondary forests are restored moist evergreen, wetland, and bamboo forests, as well as mangrove forests (comp. Pham, et al. [47]). There are also former plantations in the park [52, 93].

Due to its high plant and animal diversity, the UNESCO granted the park the status of a biosphere reserve in 2004 [51]. The plant diversity is currently estimated to comprise 1561 plant species. These belong to 842 genera. More than 400 of the species are timber species, but there are also more than 1000 medicinal, edible and ornamental species. More details on species diversity can be found in Le and Le [94]. According to the CBNP report [52] and Le [92], 29 IUCN Red List tree species have to date been identified at CBNP. Of the tree species here, 43 are listed on the Vietnam red list and account for almost 60% of all tree species in Vietnam that are in need of protection.

A large share of CBNP (~45%) is dedicated to the protection of natural dynamics in six different core zones of the park (Fig. 6). These core zones are strictly protected, which means that no management
measures are carried out. However, the accessibility to the core zones varies and data was collected in three out of the six areas along a gradient of accessibility (Fig. 6). In these areas the protection efforts were mainly directed at the conservation of the evergreen broadleaf forests. In the following, these three areas are referred to as lowland area (LLA), mid-slope area (MSA), and isolated area (ISA). The size of the areas is about 1916, 600, and 1560 ha, respectively. The accessibility follows the same order, mainly due to the elevation, whereas ISA is additionally separated from the accessible part of the park, through water (more details in Pham, et al. [47]).

**Data sampling**

We applied a simple random sampling technique [95] to set up the sample plots (Fig. 7). Each study area was divided into 30 strips. In each strip, random sample plots were generated using random numbers to determine their coordinates. Two uniform random numbers $U_{1i}$, $U_{2i}$ (the U interval from 0 to 1) were used each time to calculate $X_i = U_{1i} \times X_{\text{max}}$ with $Y_i = U_{2i} \times Y_{\text{max}}$ as coordinates for each random sample plot, and where $X_{\text{max}}$, $Y_{\text{max}}$ was the highest coordinate of the area map (Fig. 7). If the coordinate $(X_i, Y_i)$ appeared in the defined strip, this point was accepted as a sample plot point. Otherwise, the point was rejected, and the procedure was repeated with two new U(s) random values (Fig. 7).

Using this technique, we then randomly selected 30 plots within each of the three protected areas (LLA, MSA, ISA) for 90 plots in total. Each plot was 500 m² in size (20 m x 25 m).

**Standing tree layer**

We recorded all trees with DBH (diameter at breast height) $\geq$ 5 cm on the plots, respectively. Their diameter and height were measured and their identity was determined by botanical experts from the Northeast College of Agriculture and Forestry (AFC) and park employees. Not all species could be identified in the field. For these the genus or even only the family was recorded. All recorded species were assigned to categories of threat, according to the IUCN [96–99].

**Regeneration layer**

The regeneration of tree species was recorded on five subplots which were established at five positions on each sample plot (Fig. 8). Each subplot was 25 m² (5 m x 5 m) in area. Subplots were positioned in the center and the corners of the quadratic plot. Species identity of seedlings and saplings (defined as trees with DBH < 5 cm) were recorded here. Following the approach for the overstory tree species, species recorded in the regeneration layer were also assigned to categories of threat. Tree regeneration was assigned to four different height classes ($<$ 50 cm, from 50 cm – 100 cm, 100 cm – 200 cm, and $>$ 200 cm).

**Growth site characteristics**

**Topographic data**
The topographic terrain variables recorded for the whole plot were the elevation in m (T_Ele), the slope in degrees (T_sl), and the rock surface in percentage (T_RS). As measurement devices, we used an inclinometer for the slope and a GPS device (Garmin GPSMAP 64st) for coordinates and elevation. The rock surface was assessed visually on the basis of the five subplots (Fig. 8).

**Soil conditions**

Soil chemistry was derived from soil samples. An auger of 10 cm in diameter was used in the plot center to collect the samples. We only used the first 20 cm of the soil, because the nutritional status of this layer is most relevant for the plant vitality and growth in the area [100]. We took 90 soil samples in total – one sample from each plot. As variables describing soil conditions, we analyzed the samples for base saturation (S_BS) and cation exchange capacity (S_CEC), hydrolytic soil acidity (S_HA) and pH value (S_pH). In addition, the soil humus (S_SH) and the absolute soil moisture content (S_SM) were derived.

In a first step, soil samples had to be dried at room temperature and sieved through a 2 mm mesh. This procedure removed larger rocks and organic material. Then the samples were oven-dried at 105°C until constant weight was reached after about 6–8 hours. This allowed calculating the absolute soil moisture content (S_SM) by subtracting pre- and post-drying weights and dividing it by pre-drying weight. Mohr salt (K₂Cr₂O₇) was used to oxidatively determine the soil humus content (S_SH) following the Walkley and Black method [101, 102]. The hydrolytic acidity (S_HA) was determined with the Kappen method using NaOH [101–105]. Finally the cation exchange capacity (S_CEC) was determined following the Kjendhal method using Ammonium acetate (NH₄CH₃COOH) [101–105]. Here the CEC was K⁺ + Ca²⁺ + Mg²⁺ + Na⁺ + NH₄⁺ + H⁺ + Al³⁺. The ratio of the exchangeable bases (Ca²⁺, Mg²⁺, K⁺ and Na⁺) to the cation exchange capacity was defined as Base saturation (S_BS). All soil analyses were conducted at the Vietnam National University of Forestry. The soil physical variables soil texture (S_Clay, S_Sand, S_Silt) and rocks in the soil (S_RS) were also derived from the auger samples. The percentages of clay, sand, and silt were estimated with the Bouyoucos hydrometer method [106]. The percentage of rocks in the soil was estimated from a soil subsample. This subsample was sieved again and separated along the 2 mm threshold. The weight ratio was considered as percentage value. To estimate soil depth (S_SD) a steel rod was used. Soil depth per plot was defined as mean depth of five measurements across the plot (more details in Pham, et al. [47]).

**Light indicators**

Light availability was estimated by using a solariscope (SOL 300B, Ing.-Büro Behling, Wedemark) [107], which takes and automatically analyses hemispheric photographs. Measurements were conducted at 2 m above the soil surface in three diagonal subplots across the sample plot (Fig. 8). The solariscope characterizes seven properties related to light availability [107]: the direct site factor (L_DSF, representing the proportion of direct sunlight as a percent of open field conditions), the indirect site factor (L_ISF, the proportion of indirect or diffuse sunlight as a percent of open field conditions), the total site factor (L_TSF, the weighted sum of L_DSF and L_ISF as a percent of open field conditions), the gap fraction (L_GF, the proportion of uncovered gaps in a circular solid angle of 15 degrees section around the zenith), openness...
(L_OPN, weights sky areas depending on the zenith angle), leaf area index (L_LAI), and the ellipsoidal leaf area index (L_ELAD).

**Human impact**

Until present, human activities can be recorded in the park, irrespective of the protection status. Also, the park is comparably young (established in 1986) and former harvesting, slash and burn but also hunting activities affect the forest structure until today [51, 92]. Since the area is protected, a lot of effort is put into decreasing the abundance of human activities, especially in the core zones of the park. These activities even included resettlements towards outside the borders of the park. However, many villages are still located close to the park. Hence, human activities can still be detected within the park boundaries, despite them being illegal. These mainly include logging and hunting. As proxies for human activities we counted footpaths (H_FP), tree stumps (H_STP), and poacher traps to catch animals (H_AT) on the plots.

**Environmental characteristics of the study sites**

Environmental characteristics in the three study sites differed (Table 5). The average slope in ISA was twice as steep as in LLA. ISA also had the highest percentage of rock surface, followed by the MSA and LLA. The average elevation was lowest in MSA. The soil depth in LLA was deepest among the three study sites, and shallowest in ISA. MSA was characterized by more rocky soil than the other two areas. The percentage of silt and clay in MSA was highest among the three study sites; however, soil moisture was highest in ISA. Although LLA was characterized by the deepest soils, soil chemical properties revealed lower pH, less humus content and lower soil moisture than the other two areas. Light availability was comparable between the three study sites, with indirect site factors ranging between 8 and 10%. However, light availability was slightly lower in LLA compared to the other study sites. The factor L_LAI was highest in MSA, and L_ELAD was highest in ISA. Human disturbances such as footpaths and stumps occurred more frequently in LLA than in the other two sites, while most animal traps were found in MSA as compared to LLA and ISA (Table 5).
Table 5  
Environmental and human activity characteristics in three study sites (LLA, MSA and ISA) in Cat Ba National Park. The values represent mean and standard deviation of 30 plots per study site (total 90 plots). Different lower case letters indicate significant differences between the three areas (at p ≤ 0.05). We used the “multicomp” package to calculate differences between the three study sites [108]. Acronym column shows the abbreviation of the factor. T = terrain factors; S = soil properties; L = light availabilities; and H = human disturbances.

| Factors                      | Acronym | Average     | LLA   | MSA   | ISA   |
|------------------------------|---------|-------------|-------|-------|-------|
| Slope (°)                    | T_Sl    | 17.23 ± 10.71 | 13.70 ± 9.67<sup>a</sup> | 19.02 ± 10.38<sup>b</sup> | 21.85 ± 10.62<sup>c</sup> |
| Rock surface (%)             | T_RS    | 44.49 ± 31.62 | 22.71 ± 23.02<sup>a</sup> | 56.71 ± 22.84<sup>b</sup> | 71.99 ± 23.07<sup>c</sup> |
| Elevation (m)                | T_Ele   | 75.33 ± 38.92 | 78.06 ± 37.02<sup>b</sup> | 66.57 ± 37.40<sup>a</sup> | 78.35 ± 42.30<sup>c</sup> |
| Soil depth (cm)              | S_SD    | 61.78 ± 38.77 | 75.89 ± 40.24<sup>b</sup> | 51.97 ± 31.25<sup>a</sup> | 45.67 ± 32.84<sup>a</sup> |
| Rock in soil (%)             | S_SR    | 9.59 ± 15.95  | 11.31 ± 19.83<sup>b</sup> | 10.75 ± 14.96<sup>b</sup> | 5.50 ± 3.77<sup>a</sup> |
| Soil moisture (%)            | S_SM    | 8.98 ± 5.72   | 5.98 ± 5.26<sup>a</sup> | 11.06 ± 4.40<sup>b</sup> | 12.41 ± 4.72<sup>c</sup> |
| Sand (%)                     | S_Sand  | 31.45 ± 12.86 | 32.40 ± 11.26<sup>b</sup> | 24.75 ± 7.35<sup>a</sup> | 35.76 ± 16.55<sup>c</sup> |
| Silt (%)                     | S_Silt  | 40.10 ± 8.18  | 41.95 ± 7.35<sup>b</sup> | 41.73 ± 5.48<sup>b</sup> | 35.37 ± 9.62<sup>a</sup> |
| Clay (%)                     | S_Clay  | 28.45 ± 9.48  | 25.64 ± 10.47<sup>a</sup> | 33.52 ± 5.25<sup>c</sup> | 28.86 ± 8.61<sup>b</sup> |
| Soil humus content (%)       | S_SH    | 3.11 ± 1.49   | 2.67 ± 1.32<sup>a</sup> | 2.76 ± 1.24<sup>a</sup> | 4.20 ± 1.44<sup>b</sup> |
| pH                           | S_pH    | 5.10 ± 0.56   | 4.79 ± 0.50<sup>a</sup> | 5.40 ± 0.53<sup>b</sup> | 5.39 ± 0.36<sup>b</sup> |
| Hydrolytic acidity (mmol /100 g) | S_HA | 5.01 ± 2.11 | 5.12 ± 1.98<sup>b</sup> | 4.58 ± 1.97<sup>a</sup> | 5.20 ± 2.38<sup>b</sup> |
| Cation exchange capacity (mmol / 100 g) | S_CEC | 6.92 ± 1.53 | 6.12 ± 1.43<sup>a</sup> | 7.33 ± 1.11<sup>b</sup> | 7.96 ± 1.22<sup>c</sup> |
| Base saturation (%)          | S_BS    | 58.88 ± 11.66 | 55.34 ± 12.09<sup>a</sup> | 62.78 ± 11.11<sup>b</sup> | 61.64 ± 9.31<sup>b</sup> |
| Direct site factor           | L_DSF   | 11.44 ± 6.19  | 10.68 ± 5.63<sup>a</sup> | 12.14 ± 7.79<sup>b</sup> | 12.15 ± 5.31<sup>b</sup> |
### Data analysis

To visualize and contrast species diversity in the overstory and regeneration layers for the entire study area, the "iNEXT" package was used in R [109] to estimate regional tree species diversity in both forest layers. This package is based on rarefaction and extrapolation methods and estimates diversity for different Hill numbers [110]. Hill numbers (q) represent the effective number of species and increasingly weight the abundance or frequency of a species with increasing order of Hill numbers. This means that Hill numbers with q < 1 disproportionately favor infrequent species within the dataset, while all orders > 1 disproportionately favor frequent species [109, 111]. We considered the first three Hill numbers as representing widely common species diversity measures including: species richness (q = 0), true diversity of the Shannon-Index which is the exponential of the Shannon-Index (q = 1) and Simpson diversity (q = 2) [109, 111].

To investigate whether and how the overstory tree layer and the regeneration layer deviate in their tree species diversity and composition at the plot level, we also calculated species richness and the true diversity of the Shannon-Index (in the following referred to as true diversity) at the plot level. Species richness represents the total number of species per plot. Abundance and evenness of a species are accounted for in calculating the Shannon-Index as $H' = -\sum (p_i \times \ln p_i)$. Here the abundance of species i
(n_i) is divided by the total number of species (N) (\(p_i = n_i / N\)), multiplying the result with its natural logarithm (\(\ln p_i\)) [112]. We used the “vegan” package for calculating the Shannon-Index [113]. The true diversity was calculated as the exponent of the Shannon-Index (\(\exp (H')\)) [110]. By dividing plot-based richness and diversity of the regeneration layer by the respective measures of the overstory layer, we calculated several ratios (Table 6).

**Table 6**
Definition of five ratios contrasting tree species diversity in the regeneration and overstory layers.

| Ratio                        | Function | Explanation                                                                 |
|------------------------------|----------|-----------------------------------------------------------------------------|
| Species richness ratio (SRR) | \(N_r / N_o\) | \(N_r\), number of species in the regeneration layer per sample plot. \(N_o\), number of species in the overstory layer in the same sample plot. |
| True diversity ratio (TDR)   | \(T_r / T_o\) | \(T_r\), true diversity of the regeneration layer per sample plot. \(T_o\), true diversity of the overstory layer in the same sample plot. |
| Same species ratio (SSR)     | \(S_r / N_o\) | \(S_r\), number of regeneration species present in the overstory layer per sample plot. \(N_o\), see above |
| Newly occurred species ratio (NSR) | \(N_n / N_o\) | \(N_n\), number of species occurring in the regeneration layer but not in the overstory layer of a sample plot. \(N_o\), see above |
| Threatened species ratio (TSR) | \(R_r / R_o\) | \(R_r\), number of threatened tree species in the regeneration layer per sample plot. \(R_o\), number of threatened tree species in the overstory layer in the same sample plot. |

We used the one sample t-test to check the similarity in diversity or species richness between overstory and regeneration layers. We compared the ratios to the value of 1. The null hypothesis of the one sample t-test is that the mean value of each ratio is equal to 1, indicating similarity between both forest layers in terms of diversity and species richness. The alternative hypothesis is that the mean value of each ratio is less than 1, indicating a less diverse regeneration layer compared to the overstory layer [114]. Before using the one sample t-test, the ratios were tested for normality of distribution with the Shapiro-Wilk test and a nonparametric Krukal – Wallis rank sum test.

Principal component analysis (PCA) was used to extract important variables from our set of environmental variables [115]. Input data for the PCA included the 24 environmental and human factors from the 90 random sample plots. In the first step, “prcomp()”, “FactorMinorR” and “factorextra” package
were used to run the PCA [114, 116]. Then, those PCs which best explained the variation in the data based on their eigenvalues were determined. We chose the three most important PCs for further analyses.

We built linear mixed effect models with the five ratios as response variables, the PCs as fixed effects and the study area as random effect using the function “lme()” [117, 118]. The first model was built with all three PCs, then backward elimination of PCs was done using a p-value at a 5% level of significance [50]. From these we selected the best fit model using the “model.sl()” function in “MuMIn” package [119]. Simultaneously, we built the full model with the six environmental variables (EV) most strongly correlated with the first three PC axes and conducted a model selection by using the “model.sl()” function in “MuMIn” package (Barton, 2009). The study site remained as random factor. Akaike information criterion (AICc) and log-likelihood estimation (logLik) were used as criteria to choose the best fit model. Finally, criteria were compared among the best “PC” and the best “EV” model [114, 119]. We calculated the pseudo R² values to estimate the goodness of fit of the linear mixed effect model [120]. Thereby, the marginal R² indicates the explained variance by fixed effects only, whereas the conditional R² shows the explained variance by both fixed and random effects [114, 119, 120]. In addition to the five ratios, we also used the regeneration density as response variable.

All statistical analyses were conducted using the statistical software R version 3.4.2 [114]. The level of significance was defined by a p-value < 0.05.

Data collection was conducted in close cooperation with the National Park authorities and all permissions were acquired before data sampling.

**List Of Abbreviations**
| Acronym | Description |
|---------|-------------|
| CBNP    | Cat Ba National Park |
| IUCN    | The International Union for Conservation of Nature's Red List of Threatened Species |
| GOV     | Government of Vietnam |
| VACNE   | Vietnam Association for Conservation of Nature and Environment |
| iNEXT   | iNterpolation and EXTrapolation |
| DBH     | Diameter at Breast Height |
| T_SI    | Slope (°) |
| T_RS    | Rock surface (%) |
| T_Ele   | Elevation (m) |
| S_SD    | Soil depth (cm) |
| S_SR    | Rock in soil (%) |
| S_SM    | Soil moisture (%) |
| S_Sand  | Sand (%) |
| S_Silt  | Silt (%) |
| S_Clay  | Clay (%) |
| S_SH    | Soil humus content (%) |
| S_pH    | pH |
| S_HA    | Hydrolytic acidity (mmol /100 g) |
| S_CEC   | Cation exchange capacity (mmol / 100 g) |
| S_BS    | Base saturation (%) |
| L_DSF   | Direct site factor |
| L_ISF   | Indirect site factor |
| L_TSF   | Total site factor |
| L_OPN   | Openness |
| L_GF    | Gap fraction |
| L_LAI   | Leaf area index |
| L_ELAD  | Ellipsoidal leaf area distribution |
| H_FP    | Footpaths |
| H_STP   | Stumps |
| H_AT  | Animal traps             |
|-------|--------------------------|
| SRR   | Species richness ratio   |
| TDR   | True diversity ratio     |
| SSR   | Same species ratio       |
| NSR   | Newly occurred species ratio |
| TSR   | Threatened species ratio |
| PC    | Principal Component      |
| AICc  | Akaike Information Criterion |

**Declarations**

**Ethics approval and consent to participate**

Not applicable

**Consent for publication**

Not applicable

**Availability of data and materials**

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Competing interests**

The authors declare that they have no competing interests

**Funding**

This research was funded by the Vietnamese Government Scholarship (Decision No.911), and the Rufford Foundation (RSG No 21165-1), and the Department Silviculture and Forest Ecology of the Temperate Zones of the University of Göttingen. The Open Access Publication Funds of the Georg-August-University Göttingen support open access publication.

**Author Contributions**
V.V.P., C.A., P.A., and S.H. conceived the idea; V.V.P., conducted data analysis and wrote the first draft. V.V.P., C.A., P.A. and S.H finalized the manuscript. All authors have read the manuscript and agree with the content.

Acknowledgements

We are grateful for the support during field work given by the board of directors of Cat Ba National Park (Vietnam). Especially to mention are Hoang Van Thap, Nguyen Van Luc, Doan Ngoc Son, Nguyen Van Tu, Hoang Van Cau, Nguyen Van Khu, Nguyen Van Thiep. Pham Ba Su and Doan Ngoc Son helped with tree identification and Tran Thi Hang with analyzing the soil samples. We thank Kathleen Regan (USA) for linguistic corrections.

References

1. Spracklen BD, Lane JV, Spracklen DV, Williams N, Kunin WE: Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain. For Ecol Manage 2013, 310:204-212. https://doi.org/10.1016/j.foreco.2013.08.001.

2. Tyagi JV, Kumar R, Srivastava SL, Singh RD: Effect of micro-environmental factors on natural regeneration of Sal (Shorea robusta). J Forestry Res 2011, 22(4):543-550. https://doi.org/10.1007/s11676-011-0197-1.

3. Winter MB, Baier R, Ammer C: Regeneration dynamics and resilience of unmanaged mountain forests in the Northern Limestone Alps following bark beetle-induced spruce dieback. Eur J Forest Res 2015, 134(6):949-968. https://doi.org/10.1007/s10342-015-0901-3.

4. Ballabha R, Tiwari JK, Tiwari P: Regeneration of tree species in the sub-tropical forest of Alaknanda Valley, Garhwal Himalaya, India. Forest Science and Practice 2013, 15(2):89-97. https://doi.org/10.1007/s11632-013-0205-y.

5. Diaci J, Kutnar L, Rupel M, Smolej I, Urbancic M, Kraigher H: Interactions of Ecological Factors and Natural Regeneration in an Altimontane Norway Spruce (Picea abies (L.) Karst.) Stand. Phyton 2000, 40:17-26.

6. Diaci J, Rozman J, Rozman A: Regeneration gap and microsite niche partitioning in a high alpine forest: Are Norway spruce seedlings more drought-tolerant than beech seedlings? For Ecol Manage 2020, 455:117688. https://doi.org/10.1016/j.foreco.2019.117688.

7. Pokhriyal P, Uniyal P, Chauhan DS, Todaria NP: Regeneration status of tree species in forest of Phakot and Pathri Rao watersheds in Garhwal Himalaya. Curr Sci 2010, 98(2):171-175.

8. Stiers M, Willim K, Seidel D, Ammer C, Kabal M, Stillhard J, Annighöfer P: Analyzing Spatial Distribution Patterns of European Beech (Fagus sylvatica L.) Regeneration in Dependence of Canopy Openings. Forests 2019, 10(8):637. https://doi.org/10.3390/f10080637.
9. Sharma CM, Mishra AK, Tiwari OP, Krishan R, Rana YS: Regeneration Patterns of Tree Species Along an Elevational Gradient in the Garhwal Himalaya. Mt Res Dev 2018, 38(3):211. https://doi.org/10.1659/mrd-journal-d-15-00076.1.

10. Annighöfer P, Ameztegui A, Ammer C, Balandier P, Bartsch N, Bolte A, Coll L, Collet C, Ewald J, Frischbier N et al: Species-specific and generic biomass equations for seedlings and saplings of European tree species. Eur J Forest Res 2016, 135(2):313-329. https://doi.org/10.1007/s10342-016-0937-z.

11. Shrestha BB, Ghimire B, Lekhak HD, Jha PK: Regeneration of Treeline Birch (Betula utilis D. Don) Forest in a Trans-Himalayan Dry Valley in Central Nepal. Mt Res Dev 2007, 27(3):259-267. https://doi.org/10.1659/mrdd.0784.

12. Gamfeldt L, Snall T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Froberg M, Stendahl J, Philipson CD et al: Higher levels of multiple ecosystem services are found in forests with more tree species. Nat Commun 2013, 4:1340. https://doi.org/10.1038/ncomms2328.

13. Ampoorter E, Barbaro L, Jactel H, Baeten L, Boberg J, Carnol M, Castagnerol B, Charbonnier Y, Dawud SM, Deconchat M et al: Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. Oikos 2020, 129(2):133-146. https://doi.org/10.1111/oik.06290.

14. Ammer C: Konkurrenz um Licht. Zur Entwicklung der Naturverjüngung im Bergmischwald. Forstliche Forschungsberichte München 1996, 158:198.

15. Ammer C, Schall P, Wördehoff R, Lamatsch K, Bachmann M: Does tree seedling growth and survival require weeding of Himalayan balsam (Impatiens glandulifera)? Eur J Forest Res 2011, 130(1):107-116. https://doi.org/10.1007/s10342-010-0413-0.

16. Annighöfer P, Beckschäfer P, Vor T, Ammer C: Regeneration Patterns of European Oak Species (Quercus petraea (Matt.) Liebl., Quercus robur L.) in Dependence of Environment and Neighborhood. Plos One 2015, 10(8). https://doi.org/10.1371/journal.pone.0134935.

17. Aynekulu E, Denich M, Tsegaye D: Regeneration Response of Juniperus procera and Olea europaea subsp cuspidata to Exclosure in a Dry Afromontane Forest in Northern Ethiopia. Mt Res Dev 2009, 29(2):143-152. https://doi.org/10.1659/mrd.1076.

18. Bellingham PJ, Tanner EVJ, Healey JR: Sprouting of Trees in Jamaican Montane Forests, after a Hurricane. J Ecol 1994, 82(4):747-758.

19. Stanciouiu PT, O’Hara KL: Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. Eur J Forest Res 2005, 125(2):151-162. https://doi.org/10.1007/s10342-005-0069-3.

20. Boudreault C, Zouaoui S, Drapeau P, Bergeron Y, Stevenson S: Canopy openings created by partial cutting increase growth rates and maintain the cover of three Cladonia species in the Canadian boreal forest. For Ecol Manage 2013, 304:473-481. https://doi.org/10.1016/j.foreco.2013.05.043.

21. Takahashi K: Effect of Size Structure, Forest Floor Type and Disturbance Regime on Tree Species Composition in a Coniferous Forest in Japan. J Ecol 1994, 82(4):769-773.
22. Encina P, Rodríguez R, Müller-Using B, Annighöfer P, Ríos Leal D, Sáez-Carrillo K, Sánchez-Olate M: Effects of solar radiation on regeneration patterns in a Nothofagus dombeyi (Mirb.) Oerst. old-growth forest in Chile’s central-southern Andes. *Gayana Botánica* 2019, 76(1):12-23. https://doi.org/10.4067/s0717-66432019000100012.

23. Ye J, Hao Z-q, Xie P, Li J-g: Habitat associations of saplings and adults in an old-growth temperate forest in the Changbai mountains, northeastern China. *Forestry Studies in China* 2011, 13(1):13-22. https://doi.org/10.1007/s11632-011-0103-0.

24. Lusk CH, Laughlin DC: Regeneration patterns, environmental filtering and tree species coexistence in a temperate forest. *New Phytol* 2017, 213(2):657-668. https://doi.org/10.1111/nph.14168.

25. Naidu MT, Kumar OA: Tree diversity, stand structure, and community composition of tropical forests in Eastern Ghats of Andhra Pradesh, India. *Journal of Asia-Pacific Biodiversity* 2016, 9(3):328-334. https://doi.org/10.1016/j.japb.2016.03.019.

26. Sodhi NS, Koh LP, Brook BW, Ng PK: Southeast Asian biodiversity: an impending disaster. *Trends Ecol Evol* 2004, 19(12):654-660. https://doi.org/10.1016/j.tree.2004.09.006.

27. Denslow JS: Tropical rainforest gaps and tree species diversity. *Ann Rev Ecol Syst* 1987, 18:431-451.

28. Bickford D, Poo S, Posa MRC, Gower D, Johnson K, Richardson J, Rosen B, Ruber L, Williams S: Southeast Asian biodiversity crisis. 2012:434-462. https://doi.org/10.1017/cbo9780511735882.019.

29. Stibig HJ, Achard F, Carboni S, Raši R, Miettinen J: Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences* 2014, 11(2):247-258. https://doi.org/10.5194/bg-11-247-2014.

30. Sodhi NS, Posa MRC, Lee TM, Bickford D, Koh LP, Brook BW: The state and conservation of Southeast Asian biodiversity. *Biodivers Conserv* 2009, 19(2):317-328. https://doi.org/10.1007/s10531-009-9607-5.

31. Lee DK: Challenging forestry issues in Asia and their strategies. In: *The Future of Forests in Asia and the Pacific: Outlook for 2020, Proceedings of an international conference on the outlook for Asia-Pacific forests to 2020; Bangkok, Thailand.* Edited by Leslie RN. Food and Agriculture Organization of The United Nations 2009: 65-76.

32. Boukili VK, Chazdon RL: Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. *Perspect Plant Ecol Evol Syst* 2017, 24:37-47. https://doi.org/10.1016/j.ppees.2016.11.003.

33. Syaufina L, Ainuddin AN: Impacts of Fire on Southeast Asia tropical forest biodiversity: A Review. *Asian journal of Plant Sciences* 2011, 10(4):238-244.

34. Laurance WF: Forest destruction in tropical Asia. *Curr Sci* 2007, 93(11):1544-1550.

35. Giam X, Ng TH, Yap VB, Tan HTW: The extent of undiscovered species in Southeast Asia. *Biodivers Conserv* 2010, 19(4):943-954. https://doi.org/10.1007/s10531-010-9792-2.

36. Vu TP, Nguyen TML, Nguyen NL, Do DS, Nguyen XQ, Tran VL, Ngo DQ, Tran VC, Nguyen DK, Lai VC et al: Forest ecological stratification in Vietnam. In. Hanoi, Vietnam: UN-REDD Programme Vietnam; 2011: 136.
37. Sunderlin WD, Huynh TB: Poverty Alleviation and Forests in Vietnam. In. Indonesia: Subur Printing; 2005: 84.

38. Luong TH: Forest resources and forestry in Vietnam. Journal of Vietnamese Environment 2014, 6(2):171-177. https://doi.org/10.13141/jve.vol6.no2.pp171-177.

39. GOV VG: The Decision No.661/QD-TTg on objectives, tasks, policies and organization for the establishment of five million hectares of new forest. In. Hanoi, Vietnam; 1998: 11.

40. Cộng báo hiện trạng rừng toàn quốc năm 2019 [https://nongnghiep.vn/cong-bo-hien-trang-rung-toan-quoc-nam-2019-d262978.html]

41. Chien PD: Demography of threatened tree species in Vietnam. In. Utrecht University; 2006: 157.

42. Biodiversity and Conservation Vietnam [http://www.biodivn.com/2014/08/cac-vuon-quoc-gia-va-khu-bao-ton-thien-nhien-viet-nam.html]

43. Dao THH, Hölscher D: Fujian cypress and two other threatened tree species in three conservation zones of a nature reserve in north-western Vietnam. For Ecosyst 2017, 4. https://doi.org/10.1186/s40663-017-0116-9.

44. Van YT, Cochard R: Tree species diversity and utilities in a contracting lowland hillside rainforest fragment in Central Vietnam. For Ecosyst 2017, 4(1). https://doi.org/10.1186/s40663-017-0095-x.

45. Blanc L, Maury-Lechon G, Pascal JP: Structure, floristic composition and natural regeneration in the forests of Cat Tien National Park, Vietnam: an analysis of the successional trends. Journal of Biogeography, 2000, 27(1):141-157. https://doi.org/10.1046/j.1365-2699.2000.00347.x.

46. Tran VD, Ngo VC, Sato T, Binh NT, Kozan O, Thang NT, Mitlöchner R: Post-logging regeneration and growth of commercially valuable tree species in evergreen broadleaf forest, Vietnam. J Trop for Sci 2016, 28(4):426-435.

47. Pham VV, Ammer C, Annighöfer P: The Presence of IUCN Red List Tree Species in Dependence of Site Characteristics in the Vietnamese Cat Ba National Park. Diversity 2020, 12(3):104. https://doi.org/10.3390/d12030104.

48. Hooper ER, Legendre P, Condit R: Factors Affecting Community Composition of Forest Regeneration in Deforested, Abandoned Land in Panama. Ecology 2004, 85(12):3313-3326.

49. Forrester DI, Ammer C, Annighöfer PJ, Barbeito I, Bielak K, Bravo-Oviedo A, Coll L, del Río M, Drössler L, Heym M et al: Effects of crown architecture and stand structure on light absorption in mixed and monospecific Fagus sylvatica and Pinus sylvestris forests along a productivity and climate gradient through Europe. J Ecol 2018, 106(2):746-760. https://doi.org/10.1111/1365-2745.12803.

50. Annighöfer P, Seidel D, Mőlder A, Ammer C: Advanced Aboveground Spatial Analysis as Proxy for the Competitive Environment Affecting Sapling Development. Front Plant Sci 2019, 10(690):12. https://doi.org/10.3389/fpls.2019.00690.

51. CBNP CBNP: Inventory and Planning for Cat Ba National Park from 2006 to 2010 and vision to 2020. In. Haiphong, Vietnam: Cat Ba National Park; 2005: 123.
52. CBNP: **Biodiversity Information of Cat Ba National Park, Vietnam.** In. Haiphong, Vietnam: Institute of Ecology and Resources; 2007: 203.

53. Hoang VT: **Research on the current status of poor secondary forest and restoration activities in Cat Ba National Park.** Cat Ba National Park. 2018.

54. Hoang VH, Nguyen TH, Do TH: **Đặc điểm tái sinh của các loại cây gỗ trong thảm thực vật trên núi đá với thành phố Cẩm Phả (Quảng Ninh).** Tạp chí KHOA HỌC & CÔNG NGHỆ, 2017, 161(01):133 - 138.

55. Nguyen DT, C. TV, Ngo TL, Ngo NT: **Đặc điểm tái sinh tự nhiên mặt sườn loại ưu thích rừng lá rộng thường xanh tại vườn quốc gia Xuân Sơn, tỉnh Phú Thọ.** Tạp chí KHN, 2016, 3:4461 - 4468.

56. Nicotra AB, Chazdon RL, Iriarte SVB: **Spatial Heterogeneity of Light and Woody Seedling Regeneration in Tropical Wet Forests.** *Ecol Evol* 1999, 80(6):1908-1926.

57. Liu X, Lu Y, Yang Z, Zhou Y: **Regeneration and Development of Native Plant Species in Restored Mountain Forests, Hainan Island, China.** Mt Res Dev 2014, 34(4):396. https://doi.org/10.1659/mrd-journal-d-12-00110.1.

58. Osunkoya OO: **Light requirements for regeneration in tropical forest plants: Taxon-level and ecological attribute effects.** *Aust J Ecol* 1996, 21(4):429-441. https://doi.org/10.1111/j.1442-9993.1996.tb00629.x.

59. Atsbha T, Desta AB, Zewdu T: **Woody species diversity, population structure, and regeneration status in the Gra-Kahsu natural vegetation, southern Tigray of Ethiopia.** *Heliyon* 2019, 5(1):e01120. https://doi.org/10.1016/j.heliyon.2019.e01120.

60. Wright SJ: **Plant diversity in tropical forests: a review of mechanisms of species coexistence.** *Oecologia* 2002, 130(1):1-14. https://doi.org/10.1007/s004420100809.

61. Wright SJ: **The future of tropical forests.** *Year in Ecology and Conservation Biology* 2010, 2010, 1195:1-27. https://doi.org/10.1111/j.1749-6632.2010.05455.x.

62. Laurance WF, Oliveira AA, Laurance SG, Condit R, Nascimento HEM, Sanchez-Thorin AC, Lovejoy TE, Andrade A, D’Angelo S, Ribeiro JE et al: **Pervasive alteration of tree communities in undisturbed Amazonian forests.** *Nature* 2004, 428:171-175. https://doi.org/https://doi.org/10.1038/nature02383.

63. Janzen DH: **Herbivores and the Number of Tree Species in Tropical Forests.** *The American Naturalist* 1970, 104(940):501-528. https://doi.org/10.1086/282687.

64. Karsten RJ, Jovanovic M, Meilby H, Perales E, Reynel C: **Regeneration in canopy gaps of tierra-firme forest in the Peruvian Amazon: Comparing reduced impact logging and natural, unmanaged forests.** *For Ecol Manage* 2013, 310:663-671. https://doi.org/10.1016/j.foreco.2013.09.006.

65. Christie DA, Armesto JJ: **Regeneration Microsites and Tree Species Coexistence in Temperate Rain Forests of Chiloé Island, Chile.** *J Ecol* 2003, 91(5):776-784.

66. Löf M, Ammer C, Coll L, Drössler L, Huth F, Madsen P, Wagner S: **Regeneration Patterns in Mixed-Species Stands.** 2018, 31:103-130. https://doi.org/10.1007/978-3-319-91953-9_4.

67. Skowronek S, Terwei A, Zerbe S, Mölder I, Annighöfer P, Kawaletz H, Ammer C, Heilmeier H: **Regeneration Potential of Floodplain Forests Under the Influence of Nonnative Tree Species: Soil...**
68. Zackrisson O, Nilsson M-C, Steijlen I, Hornberg G: Regeneration Pulses and Climate-vegetation Interactions in Nonpyrogenic Boreal Scots Pine Stands. *J Ecol* 1995, **83**(3):469-483.

69. McLaren KP, McDonald MA: Seedling dynamics after different intensities of human disturbance in a tropical dry limestone forest in Jamaica. *J Trop Ecol* 2003, **19**:567-578. https://doi.org/10.1017/S026647403003626.

70. Cerdà A, García-Fayos F: The influence of seed size and shape on their removal by water erosion. *Catena* 2002, **48**:293-301.

71. Jiao J, Han L, Jia Y, Wang N, Lei D, Li L: Can seed removal through soil erosion explain the scarcity of vegetation in the Chinese Loess Plateau? *Geomorphology* 2011, **132**(1-2):35-40. https://doi.org/10.1016/j.geomorph.2011.04.033.

72. Stevenson PR, Aldana AM, Cardenas S, Negret PJ: Flooding and soil composition determine beta diversity of lowland forests in Northern South America. *Biotropica* 2018, **50**(4):568-577. https://doi.org/10.1111/btp.12541.

73. Araújo FDC, Tng DYP, Apagua DMG, Morel JD, Pereira DGS, Santos PF, Santos RMd, Collins B: Flooding regime drives tree community structure in Neotropical dry forests. *J Veg Sci* 2019, **30**(6):1195-1205. https://doi.org/10.1111/jvs.12800.

74. Bazzaz FA: Tropical forests in a future climate: Changes in biological diversity and impact on the global carbon cycle. *Clim Change* 1998, **39**(2-3):317-336. https://doi.org/Doi 10.1023/A:1005359605003.

75. Uriarte M, Muscarella R, Zimmerman JK: Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biol* 2018, **24**(2):E692-E704. https://doi.org/https://doi.org/10.1111/gcb.14000.

76. Liu J, Ashton PS: Simulating Effects of Landscape Context and Timber Harvest on Tree Species Diversity. *Ecol Appl* 1999, **9**(1):186-201.

77. Dalling JW, Tanner EVJ: An Experimental Study of Regeneration on Landslides in Montane Rain Forest in Jamaica. *J Ecol* 1995, **83**(1):55-64.

78. He SY, Zhong YL, Sun YD, Su ZY, Jia XR, Hu YQ, Zhou Q: Topography-associated thermal gradient predicts warming effects on woody plant structural diversity in a subtropical forest. *Sci Rep-Uk* 2017, **7**. https://doi.org/10.1038/Srep40387.

79. Lan GY, Hu YH, Cao M, Zhu H: Topography related spatial distribution of dominant tree species in a tropical seasonal rain forest in China. *For Ecol Manage* 2011, **262**(8):1507-1513. https://doi.org/10.1016/j.foreco.2011.06.052.

80. Liu J, Yunhong T, Slik JWF: Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest. *For Ecol Manage* 2014, **330**:75-81. https://doi.org/10.1016/j.foreco.2014.06.045.
81. Dayananda SK, Mammides C, Lee M-B, Liu J-J, Pasion BO, Sreekar R, Yasuda M, Quan R-C, Slik JWF, Tomlinson KW et al: Topography and soil type are critical to understanding how bird and herpetofaunal communities persist in forest fragments of tropical China. *Biol Conserv* 2017, 215:107-115. https://doi.org/10.1016/j.biocon.2017.08.034.

82. Poulos HM, Camp AE: Topographic influences on vegetation mosaics and tree diversity in the Chihuahuan Desert Borderlands. *Ecology* 2010, 91(4):1140-1151. https://doi.org/10.1890/08-1808.1.

83. Liu J, Tan YH, Slik JWF: Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest. *For Ecol Manage* 2014, 330:75-81. https://doi.org/10.1016/j.foreco.2014.06.045.

84. Aiba S-i, Kitayama K, Takyu M: Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. *Plant Ecol* 2004, 174(1):147-161. https://doi.org/Doi 10.1023/B:Vege.0000046059.92806.49.

85. Szewczyk J, Szwagrzyk J: Tree regeneration on rotten wood and on soil in old-growth stand. *Vegetatio* 1996, 122:37-46.

86. Puerta-Piñero C, Muller-Landau HC, Calderón O, Wright SJ: Seed arrival in tropical forest tree fall gaps. *Ecology* 2013, 94(7):1552-1562.

87. Rüger N, Huth A, Hubbell SP, Condit R: Response of Recruitment to Light Availability across a Tropical Lowland Rainforest Community. *J Ecol* 2009, 97(6):1360-1368. https://doi.org/10.1111/j.1365-2745.2009.01552.x.

88. Carlton GC, Bazzaz FA: Resource Congruence and Forest Regeneration following an Experimental Hurricane Blowdown. *Ecology* 1998, 79(4):1305-1319.

89. van Gemerden BS, Olff H, Parren MPE, Bongers F: The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J Biogeogr* 2003, 30(9):1381-1390. https://doi.org/DOI 10.1046/j.1365-2699.2003.00937.x.

90. Chazdon RL: Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect Plant Ecol Evol Syst* 2003, 6(1-2):51-71. https://doi.org/10.1078/1433-8319-00042.

91. Cat Ba National Park [http://www.vacne.org.vn/vuong-quoc-gia-cat-ba/2842.html]

92. Le MT: *Flora in Cat Ba National Park*. In. Hanoi, Vietnam: Forest Inventory and Planning Institute; 2006: 17.

93. Carle J, Holmgren P: Definitions related to planted forests In. *FAO*; 2003: 16.

94. Le MC, Le TH: *List of vascular plants in Cat Ba National Park*. In. Haiphong, Vietnam: Vietnam National Forestry University; 2005: 47.

95. Kleinn C, Yihlam T, Yang H, Schnell SB, Netra, Fehrmann L: *Forest Inventory*, 2 edn. Goerg August Universität Göttingen; 2009.

96. Vietnam forest creatures [http://www.vncreatures.net/e_tracuu.php]

97. The IUCN Red List of Threatened Species [http://www.iucnredlist.org/]

98. Vietnam Plant Data Center [http://www.botanyvn.com/?lg=en]
99. Nguyen TB, Tran DL, Nguyen T, Vu VD, Nguyen NT, Nguyen VT, Nguyen KK: *Vietnam Red Data Book - Part II. Plant*. In: *Vietnam Red Data Book*. vol. II. Hanoi, Vietnam: Publisher of science and technology; 2007.

100. Nguyen TV, Mitlohner R, Nguyen VB, Tran VD: *Environmental Factors Affecting the Abundance and Presence of Tree Species in a Tropical Lowland Limestone and Non-limestone Forest in Ben En National Park, Vietnam*. *Journal of Forest and Environmental Science* 2015, 31(3):177-191. https://doi.org/10.7747/jfes.2015.31.3.177.

101. Le VD: *Soil Science*. In. Nong Lam University: Ho Chi Minh City, Vietnam; 2009: 151.

102. Ha QK: *Forest soil science*. Vietnam National University of Forestry; 2002.

103. Delgado A, Gómez JA: *Chapter 2 The Soil. Physical, Chemical and Biological Properties*. In: *Principles of Agronomy for Sustainable Agriculture*. Springer; 2016: 13-26. https://doi.org/10.1007/978-3-319-46116-8_2.

104. Le TB: *Soil Science*. In. University of Agriculture and Forestry: Hue University; 2009: 151.

105. Carter MR, Gregorich EG: *Soil Sampling and Methods of Analysis*. In., vol. Second Edition: CRC Press, Taylor & Francis Group; 2006: 1240.

106. Beretta AN, Silbermann AV, Musselli R, Paladino L, Torres D, Bassahun D, Musselli R, García-Lamothe A: *Soil texture analyses using a hydrometer: modification of the Bouyoucos method*. *Cienc Inv Agr* 2014, 41(2):263-271. https://doi.org/10.4067/S0718-16202014000200013.

107. Behling I-B: *Solariscope SOL 300 Reference Manual*. In. Edited by Behling I-B. Germany; 2018.

108. Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A, Scheibe S: *Simultaneous Inference in General Parametric Models*. 2019.

109. Hsieh TC, Ma KH, Chao A, McInerny G: *iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers)*. *Methods Ecol Evol* 2016, 7(12):1451-1456. https://doi.org/10.1111/2041-210x.12613.

110. Jost L: *Entropy and diversity*. *Oikos* 2006, 113(2):363-375.

111. Chao A, Jost L: *Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size*. *Ecology* 2012, 93(12):2533-2547. https://doi.org/10.2307/41739612.

112. Shannon CE: *A mathematical theory of communication*. *Bell Systems Technological Journal* 1948, 27:379-423.

113. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P *et al*: *Community Ecology Package*. 2019.

114. R: *A language and environment for statistical computing* [http://www.R-project.org.]

115. Abdi H, Williams LJ, Valentin D: *Multiple factor analysis: principal component analysis for multitable and multiblock data sets*. *Wiley Interdisciplinary Reviews: Computational Statistics* 2013, 5(2):149-179. https://doi.org/10.1002/wics.1246.

116. Husson F, Josse J, Le S, Mazet J: *Package ‘FactoMineR’*. In.; 2017. https://doi.org/10.1201/b10345-2>.
117. Bates D, Mächler M, Bolker BM, Walker SC: Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 2015. https://doi.org/10.18637/jss.v067.i01.

118. Winter B: Linear models and linear mixed effects models in R with linguistic applications. In. University of California, Merced, Cognitive and Information Sciences; 2014.

119. Barton K: Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18. In.; 2009.

120. Johnson PCD: Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. Methods Ecol Evol 2014, 5:944-946. https://doi.org/10.1111/2041-210X.12225.