Mechanisms Maintaining Biomass Stability in Woody Species Communities in Evergreen Broadleaved Forests of Dong Nai Culture and Nature Reserve, Dong Nai province, Southern Vietnam

Nguyen Van Quy[1], Le Van Cuong[2], Vu Manh[1], Nguyen Thi Van[1], Nguyen Van Hop[2], Nguyen Thanh Tuan[2], Nguyen Hong Hai[3]*

[1]Southern Branch of Joint Vietnam - Russia Tropical Science and Technology Research Center
[2]Vietnam National University of Forestry - Dong Nai Campus
[3]Vietnam National University of Forestry

Cơ chế duy trì sự ổn định sinh khối trong quần xã cây gỗ của rừng lá rộng thường xanh ở Khu Bảo tồn Thiên nhiên và Văn hóa Đồng Nai, tỉnh Đồng Nai

Nguyễn Văn Quý[1], Lê Văn Cường[2], Vũ Mạnh[1], Nguyễn Thị Vân[1], Nguyễn Văn Hợp[2], Nguyễn Thanh Tuấn[2], Nguyễn Hồng Hải[3]*

[1]Trung tâm nhiệt đới Việt - Nga, Chi nhánh phía Nam
[2]Trường Đại học Lâm nghiệp - Phân hiệu Đồng Nai
[3]Trường Đại học Lâm nghiệp
**Corresponding author: hainh@vnuf.edu.vn*

https://doi.org/10.55250/jo.vnuf.9.2.2024.043-054

Article info:
Received: 14/06/2024
Revised: 19/07/2024
Accepted: 20/08/2024

Keywords:
Biodiversity, community stability, dominant species, species asynchrony, theoretical ecology.

ABSTRACT

Tropical forest ecosystems experience dynamic changes in response to environmental fluctuations and disturbances. Understanding the mechanisms governing their stability is crucial for maintaining ecosystem services. Among these ecosystems, evergreen broadleaved forests play a pivotal global role. This study investigates the impacts of overyielding, stand structure, species asynchrony, and the stability of dominant species on community biomass stability (CBS) within the Dong Nai Culture and Nature Reserve's evergreen broadleaved forests. The study utilized species richness, diameter-at-breast-height (DBH) variation coefficient, species asynchrony, and stability of dominant species as explanatory variables. The response variables included CBS, mean biomass (μ), and biomass standard deviation (σ). Three structural equation models (SEMs) were constructed to assess the relative strengths of direct and indirect effects among these variables. The results indicated that: (1) The SEMs achieved a good fit, explaining 41.8% of the variance in CBS. (2) Species richness negatively correlated significantly with μ (path coefficient = -0.112) and σ (-0.056). (3) DBH variation coefficient showed significant negative correlations with CBS (-0.161) and μ (-0.087). (4) Species asynchrony exhibited significant positive correlations with CBS (0.061), μ (0.076), and σ (0.061). (5) Dominant species stability showed significant positive correlations with CBS (0.588) and μ (0.153) and a negative correlation with σ (-0.588). These findings underscore that while stand structure and species asynchrony significantly influence CBS in evergreen broadleaved forests, the stability of dominant species emerges as the primary predictor of CBS. Therefore, effective forest management strategies should prioritize conserving and enhancing conditions that support dominant species, ensuring the sustainability of forest ecosystems in the study area.

Từ khóa:
Đa dạng sinh học, loài ưu thế, sinh thái lý thuyết, sự ổn định của quần xã, tính không đồng bộ của các loài

TÓM TẮT

Nghiên cứu này được thực hiện nhằm điều tra ảnh hưởng của năng suất vượt trội, cấu trúc lâm phần, tính không đồng bộ loài và sự ổn định của các loài ưu thế đối với sự ổn định sinh khối (BS) của các loài cây gỗ trong rừng lá rộng thường xanh ở Khu Bảo tồn Thiên nhiên và Văn hóa Đồng Nai, tỉnh Đồng Nai. Các chỉ số độ giàu loài (Sri), hệ số biến thiên đường kính (Var), tính không đồng bộ của loài (Sas) và độ ổn định của các loài ưu thế (Dss) đã được sử dụng làm các biến giải thích. Trong khi đó, độ ổn định sinh khối (BS), sinh khối trung bình (μ) và độ lệch chuẩn sinh khối (σ) của các lâm phần được sử dụng làm biến phụ thuộc. Ba mô hình cấu trúc tuyến tính (SEMs) đã được xây dựng để so sánh mức độ ảnh hưởng trực tiếp và gián tiếp giữa *các biến. Kết quả cho thấy: (1) Mức độ phù hợp của SEMs ở mức tốt, giải thích 41,8% phương sai của BS; (2) Sri tương quan nghịch có ý nghĩa thống kê với μ (hệ số đường dẫn là -0,112) và σ (-0,056); (3) Var tương quan nghịch có ý nghĩa thống kê với BS (-0,161) và μ (-0,087); (4) Sas tương quan thuận có ý nghĩa thống kê với BS (0,061), μ (0,076) và σ (0,061); (5) Dss tương quan thuận có ý nghĩa thống kê với BS (0,588) và μ (0,153) và tương quan nghịch có ý nghĩa thống kê với σ (-0,588). Những phát hiện này chỉ ra rằng, sự ổn định của các loài ưu thế là yếu tố ảnh hưởng nhiều nhất đến sự ổn định của các quần xã rừng lá rộng thường xanh.*

1. INTRODUCTION

The escalating impact of climate change exacerbates the frequency and severity of extreme weather events, posing significant threats to forests' growth and long-term sustainability worldwide [1]. This issue is particularly concerning for tropical forests, where deforestation shows no signs of abating. Such peril undermines the vital role of forests as carbon sinks and critical allies in the fight against climate change [2]. Consequently, ensuring forest stability, characterized by their capacity to withstand and function effectively under environmental pressures, is emerging as a central priority in contemporary forest management strategies.

Ecologists have proposed various mechanisms to elucidate species diversity's significance in enhancing ecosystem processes' temporal stability. One of these mechanisms is overyielding, where the biomass of a community increases due to functional complementarity among species or the dominance of more productive species [3]. This phenomenon enhances ecosystem stability by amplifying mean biomass output more than variability. Another crucial mechanism is species asynchrony, characterized by species' staggered, dynamic responses to environmental changes facilitated by niche differentiation [4]. Recent studies underscore the critical role of this asynchronous behaviour in maintaining the stability of species diversity, with intra-specific variability providing additional support for community stability [5].

On the contrary, specific theories propose that ecosystem stability is primarily determined by dominant species rather than species diversity [6]. This viewpoint aligns with Grime's mass ratio hypothesis, which suggests that dominant species exert greater control over ecosystem functions, including stability, in the short term [7]. Both common and rare species are believed to enhance long-term stability by bolstering the resilience of dominant species. This hypothesis is supported by numerous studies, revealing a nuanced interaction between the dominance of specific species and the overall diversity of species in maintaining ecological stability [5, 8, 9].

Numerous authors have extensively explored the effects of various factors such as species richness, phylogenetic diversity, species asynchrony, stability of dominant species, and environmental shifts on the temporal stability of grassland communities [10]. Forest ecosystems, crucial habitats supporting diverse species, provide many ecosystem services essential for human societies [11]. These ecosystems undergo temporal fluctuations in response to environmental changes and disturbances, emphasizing the need to understand the mechanisms that maintain forest stability amidst global shifts [12]. Despite its importance, there is a need for more studies investigating how biotic and abiotic factors specifically influence the stability of forest communities, where community composition evolves slowly and potentially impacts broader temporal stability [5]. Several studies suggest species diversity enhances forest stability and improves ecosystem functioning and services [13]. While the impact of species diversity on stability is well-documented, research on structural diversity—measured by metrics such as the Gini coefficient, standard deviation, and coefficient of variation of tree diameters at breast height—is relatively limited but indicates significant effects on forest productivity [14]. Furthermore, additional investigation is warranted into the roles of species asynchrony and stability of dominant species in forest community stability [5].

The present study will investigate the factors influencing the resilience of natural stands within the evergreen broadleaved forest of Dong Nai Culture and Nature Reserve, focusing on overyielding, stand structure, species asynchrony, and the stability of dominant species. The study's primary objective is to assess the temporal consistency of productivity within the woody tree community. Due to limitations in survey data availability, the temporal stability of above-ground biomass (AGB) is used as a surrogate indicator, termed community biomass stability. Three structural equation models were developed to uncover the underlying mechanisms supporting community stability. These models incorporate explanatory variables such as overyielding (measured by species richness), stand structure (evaluated by the coefficient of variation in breast height diameter), species asynchrony, and the stability of dominant species. The analysis results facilitate a comprehensive evaluation of the direct and indirect effects, as well as their interrelationships, of overyielding, stand structure, species asynchrony, and the stability of dominant species on the AGB stability of woody species in the evergreen broadleaved forest of the study area.

2. RESEARCH METHODS

2.1. Study area

The study was conducted in the evergreen broadleaved forest of Dong Nai Culture and Natural Reserve, situated in Dong Nai province, Southern Vietnam. The reserve's geographical coordinates range from 11º05’10’’ to 11º22’31’’ North latitude and from 106º54’19’’ to 107º09’03’’ East longitude. Covering a total natural area of 100,572 ha, the Dong Nai Cultural Natural Reserve comprises 68,052 ha of forest and forestry land, with a flooded area of 32,520 ha. The study area features a tropical monsoon climate, characterized by distinct dry and rainy seasons and minimal impact from natural disasters. The terrain is relatively flat, with an average elevation of 105 m *a.s.l.* and slopes ranging from 5 to 20º.

The plant community in the study area is predominantly composed of species from the Dipterocarpaceae, Myrtaceae, Ebenaceae, and Sapindaceae families [15]. Our study consisted of two field surveys: one conducted in 2019 and another in 2024, each lasting four months.

2.2. Data collection

In 2019, three permanent 1-ha plots were established within Dong Nai Culture and Natural Reserve at the following coordinates: Plot 1 - 11º17'5.14" N, 107º2'25.44" E; Plot 2 - 11º15'5.18" N, 106º59'51.65" E; and Plot 3 - 11º13'15.02" N, 107º2'28.72" E. Each plot was subdivided into 25 subplots, each measuring 20 m by 20 m. All woody trees with a DBH of at least 5 cm within these plots were meticulously measured, mapped, identified, and tagged. The initial census recorded a total of 3,497 stems comprising 98 species from 39 families and 77 genera.

In 2024, a follow-up census using the same methodology was conducted, documenting any new arrivals or deaths of individuals. Importantly, there were no significant natural disturbances within the plots throughout the study period.

2.3. Identification of tree species

Tree species were identified using the comparative morphology method, with reference to "An Illustrated Flora of Vietnam" and "Timber Trees Resources in Vietnam" [16, 17]. Scientific nomenclature was verified and corrected using databases from Kew Royal Botanic Gardens (*http://www.plantsoftheworldonline.org*) and World Flora Online (*http://104.198.148.243*).

2.4. Data analysis

2.4.1. Tree above-ground biomass

The above-ground biomass (AGB) of trees in subplots was estimated using the following equation [18].

$$AGB = \exp(-2.024-0.896\times E + 0.920\times \log(WD)+2.795\times \log(DBH)-0.0461\times(\log(DBH)^2)) \quad (1)$$

In Equation 1, wood density (WD) data were sourced from the global wood density database. The environmental stress factor (E) was determined based on the geographical coordinates of the study sites.

2.4.2. Community stability

Community stability, which indicates the temporal consistency of a community, was quantified as the inverse of the coefficient of variance of AGB recorded across two distinct time periods: the 2019 and 2024 surveys conducted within individual 1-ha plots. Initially, AGB values were determined for every tree with a minimum DBH of 5 cm during both surveys, using a site-specific model tailored for this study. Subsequently, the stability of the community within each subplot of the 1-ha plot was calculated using Equation 2 [5]:

$$\text{Stability} = \frac{\mu}{\sigma} \quad (2)$$

Where, μ and σ represent the mean and standard deviation of AGB calculated within each subplot over the five-year span, respectively.

2.4.3. Stability of dominant species

The study also assessed the stability of dominant species by using biomass-time stability metrics [5]. Initially, tree species were ranked based on their AGB, with the top nine species identified as *Shorea thorelii, Nephelium cuspidatum, Dipterocarpus alatus, Swietenia mahogani, Syzygium fastigiatum, Elaeocarpus japonicus, Diospyros venosa, Colona auriculata,* and *Terminalia bellirica*. Together, these species accounted for 62.63% of the total AGB, with individual contributions ranging from 3.05% to 16.16%. To calculate the biomass of these dominant species in each subplot, the biomass of all individuals (including deceased ones) belonging to these species within the subplot was aggregated. Subsequently, the stability of dominant tree species within each subplot was determined by computing the ratio of the mean biomass to the standard deviation of biomass measurements taken twice for each dominant species.

2.4.4. Overyielding and species asynchrony

The concept of overyielding, a critical aspect of species diversity, plays a significant role in influencing the stability of community biomass. In this study, we assessed overyielding by quantifying species richness, which denotes the number of species within a specified subplot.

Species asynchrony occurs when changes in the abundance of one species are counterbalanced by changes in other species. This compensation primarily results from diverse responses among species with different functional traits to environmental changes and interspecific competition. To calculate species asynchrony for each subplot, Equation 3 was utilized [9].

$$\text{Species asynchrony} = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{N}\sigma_i\right)^2} \quad (3)$$

In Equation 3, σ^2 signifies the variance of community AGB within a 20 m × 20 m subplot, while σ_i represents the standard deviation of AGB for a specific species i in a community comprising N species throughout the period from 2019 to 2024. Species asynchrony is assessed on a scale ranging from 0, indicating complete synchrony, to 1, denoting complete asynchrony.

The diversity within forest stand structures is primarily assessed through the variation in DBH [19]. In this study, we employed the methodology outlined by Schnabel et al. [13] to compute three metrics indicative of forest stand structure diversity: DBH standard deviation, DBH coefficient of variation, and DBH Gini coefficient (Eq. 4). Additionally, we utilized the basal area per hectare (m^2 ha^{-1}) as a measure of stand density, reflecting the spatial distribution of trees within the forest. Given the significant variation in tree sizes within natural forests, the use of the number of trees per hectare as a measure of stand density would lead to considerable errors.

$$SD_D = \sqrt{\frac{\sum_{i=1}^{N}(DBH_i - \overline{DBH})^2}{N-1}}; \quad Var_D = \frac{SD_D}{\overline{DBH}}; \quad Gini_D = 100\% \frac{\sqrt{\frac{(DBH_i - \overline{DBH})^2}{N}}}{\overline{DBH}} \quad (4)$$

where,

SD_D stands for the standard deviation of DBH;

Var_D represents the coefficient of variation of DBH;

and $Gini_D$ indicates the Gini coefficient of DBH.

Additionally, N denotes the total number of individuals within the subplot; DBHi represents the DBH value of the i-th individual within the subplot, and DBH signifies the average DBH of all individuals within the subplot.

2.4.5. Statistical analysis

Before delving into statistical analysis, the final response variables, comprising community biomass and its two constituents (μ and σ), underwent logarithmic transformation with a base of 10. This transformation was applied to adhere to the assumptions of linearity and normality. Subsequent to this transformation, all variable observations were centralized to mitigate deviations from normality and ensure comparability across variables within a similar range. The variance inflation factor (VIF) was then calculated using the "CAR" package within the R software. A criterion of VIF < 5 was employed to detect and eliminate multicollinear variables from the multiple regression model. The selected indicators for analysis included species richness, the standard deviation of DBH, the coefficient of variation of DBH, stand density, species asynchrony, and the stability of dominant species.

Utilizing structural equation modeling (SEM), we investigated how specific variables influence the stability of community biomass. To accomplish this, we partitioned community biomass stability into two components (referred to as μ and σ), which acted as response variables in constructing two separate SEMs. These models were designed to uncover the underlying mechanisms that govern community stability. The adequacy of the SEMs was assessed using various metrics, including the goodness-of-fit index (GFI), Chi-Square test, and standardized root mean square residual (SRMR). A model was considered acceptable if it satisfied the following criteria: a non-significant Chi-Square test ($p > 0.05$), GFI >0.95, and SRMR < 0.08 . The SEMs were developed using the Lavaan package within R software version 4.3.3. Throughout the modeling process, variables that exhibited poor fit were eliminated, retaining explanatory variables such as species richness, coefficient of variation of DBH, species asynchrony, and stability of dominant species. Ultimately, we calculated standardized direct, indirect, and total effects, along with their corresponding p-values, to elucidate their impacts on community biomass stability and its constituent components.

Three multiple regression models were developed to enhance interpretability and enable comparisons. The focus remained on community biomass stability and its two constituent components as response variables. Unlike structural equation modeling, these regression models included additional explanatory variables such as the standard deviation of DBH and stand density. However, due to the complexity of capturing interactions among variables in multiple regression, the primary emphasis was on the insights gleaned from structural equation modeling. The multiple regression models served as supplementary analyses to complement the main findings.

3. RESULTS

The results of the multiple regression model analysis, as shown in Figure 1, revealed several significant findings. Firstly, there was a clear positive correlation observed between species richness and both μ and σ (Fig. 1b, c). Particularly, the correlation with μ (standardized coefficient = 0.18) showed a significantly stronger association compared to σ (standardized coefficient = 0.13). In contrast, no statistically significant correlation was found with biomass stability (standardized coefficient = 0.04).

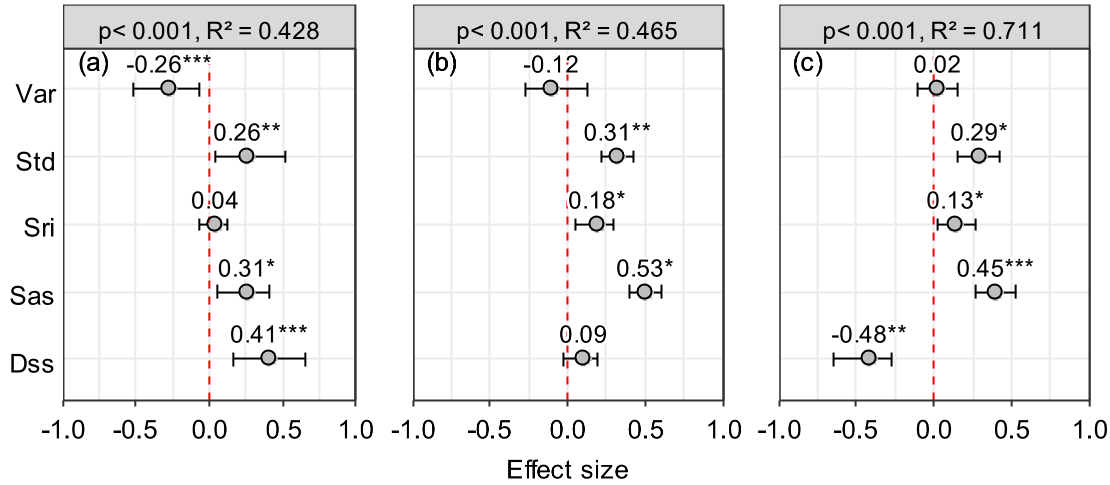

Figure 1. The influence of predictor variables on community biomass stability (a), mean biomass (b), and biomass standard deviation (c) within the evergreen broadleaf forests of Dong Nai Culture and Nature Reserve is examined using multiple regression analyses

(The predictor variables include Sri (species richness), Dss (dominant species stability), Sas (species asynchrony), Var (coefficient of variation of DBH), and Std (stand density). The grey points indicate the average estimates from the models, and the grey bars denote the 95% confidence intervals.
The red dashed line indicates the effect that intersects with 0, representing neutrality.
*Levels of statistical significance are indicated as *, p < 0.05; **, p < 0.01; ***, p < 0.001)*

Upon examining the coefficient of variation of DBH, it indicated a notable negative correlation with biomass stability (-0.26), as well as negative correlations with μ (-0.12), and a positive correlation with σ (0.02). However, these relationships did not reach statistical significance for μ and σ. Furthermore, stand density exhibited a significant positive correlation with biomass stability (0.26), showing robust positive correlations with both components of biomass stability (standardized coefficients = 0.31 for μ and 0.29 for σ). Similarly, species asynchrony demonstrated a substantial positive correlation with biomass stability (0.31) and its associated components (standardized coefficients = 0.53 for μ and 0.45 for σ).

Of particular interest, dominant species stability emerged as significantly positively correlated with community biomass stability, with the highest standardized coefficient (0.41), surpassing the correlation observed with species asynchrony (0.31). Moreover, dominant species stability showed a notable negative correlation with σ, presenting the most substantial standardized coefficient (-0.48), although this difference was relatively minor compared to species asynchrony (0.45). Unexpectedly, no significant correlation was found between μ and dominant species stability, as indicated by a low standardized coefficient (0.09), markedly lower than that of species asynchrony (0.53).

The SEM demonstrated a good fit, explaining 41.8% of the variance in community biomass stability through the observed variables (Fig. 2a). However, substituting community biomass stability with μ and σ individually resulted in a notable decrease in explanatory power, to 5.1% (Fig. 2b) and 35.6% (Fig. 2c), respectively. This indicates that σ plays a more significant role in influencing changes in community biomass stability compared to μ. Importantly, species asynchrony showed substantial positive correlations with both overall community biomass stability and its constituent components, with path coefficients of 0.061, 0.076, and 0.061, respectively. These findings suggest that species asynchrony primarily enhances community biomass stability by augmenting μ.

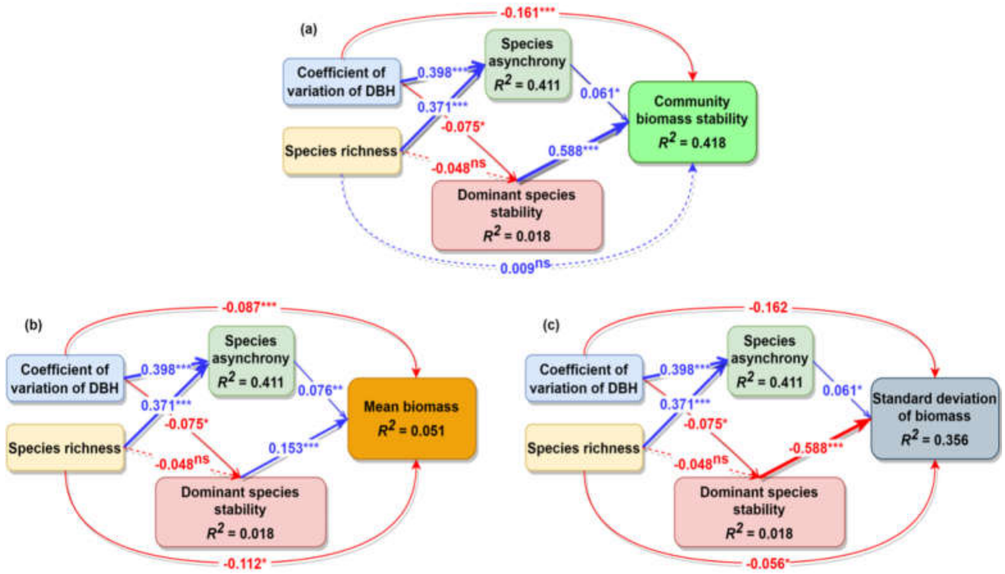

Figure 2. SEMs was employed to evaluate the influence of several variables—species richness, variation in tree DBH, species asynchrony, and stability of dominant species—on community biomass dynamics in an evergreen broadleaf forest. The analysis focused on three aspects: biomass stability (a), mean biomass (b), and biomass variability (c)

*(The results indicated a p-value of 0.586, a CFI of 1.000, and a SRMR of 0.002. Statistically significant relationships are denoted by solid arrows, and non-significant ones by dashed arrows, with blue arrows signifying positive impacts and red arrows negative. Each arrow is labeled with a standardized regression coefficient, the arrow's thickness reflecting the magnitude of the coefficient. The R^2 values represent the explained variance. Levels of significance are indicated as follows: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, non-significant)*

The results from the SEM revealed significant positive correlations between species richness, coefficient of variation of DBH, and species asynchrony, with path coefficients of 0.398 and 0.371, respectively. These factors indirectly impacted community biomass stability through their influence on species asynchrony. Additionally, dominant species stability exhibited a substantial positive correlation with community biomass stability, with a path coefficient of 0.588, indicating a stronger relative influence compared to species asynchrony. Furthermore, it showed a significant positive correlation with μ (path coefficient = 0.153), a magnitude similar to that of species asynchrony, and a significant negative correlation with σ (path coefficient = -0.588), exerting a notably greater influence than species asynchrony. The results underscored the significantly greater relative impact of dominant species stability on community biomass stability compared to that of species asynchrony.

Moreover, species richness and coefficient of variation of DBH exhibited inverse correlations with dominant species stability, with the coefficient of variation of DBH showing a significant association (path coefficient = -0.075), whereas species richness did not (path coefficient = -0.048). This suggests that the forest stand's structure indirectly influenced community biomass stability through its effect on dominant species stability.

4. DISCUSSION

4.1. The influence of stand structure on community biomass stability surpasses overyielding

The stability of community biomass was influenced by both species diversity and stand structure [14]. However, our findings emphasized the predominant impact of stand structure on community biomass stability. This underscores the central role played by structural diversity in maintaining biomass stability within evergreen broadleaved forests. The complex distribution of tree sizes is believed to enhance the efficiency of light capture and utilization [20]. Furthermore, the coefficient of variation of DBH emerged as a crucial indicator of tree size heterogeneity, with higher values indicating greater unevenness in tree sizes, potentially leading to increased instability in growth rates and subsequent reductions in community biomass stability [21].

Although the significance of overyielding (species richness) lacked statistical support, it does not diminish the overall importance of species diversity. The results reveal that species diversity directly affects community biomass stability by statistically influencing the mean more than the standard deviation of biomass, consistent with findings in grassland ecosystems [22]. Additionally, species diversity indirectly bolsters community biomass stability by promoting species asynchrony, a conclusion supported by multiple studies [5, 13]. Nevertheless, meta-analyses, including the comprehensive study conducted by Gross et al. [23], suggest that community biomass stability may decline with increasing species diversity. In such cases, promoting species asynchrony becomes crucial in offsetting the decrease in community biomass stability and sustaining ecosystem stability within highly diverse communities [24]. This assertion aligns with the mass-ratio hypothesis, which suggests that the management and protection of forest ecosystems should focus not only on biodiversity but also on community structural attributes [7].

4.2. Significant influence of species asynchrony on community biomass stability and its components

Species asynchrony is strongly and positively linked to the stability of community biomass, thereby improving it by mitigating the impact of declining biomass in one species through compensatory increases in others [5]. In natural forests, changes in biomass are frequently initiated by small-scale disturbances, such as the demise of large trees, which result in heightened canopy openings and increased light penetration [25]. When forests host a variety of species exhibiting high levels of asynchrony, these openings are promptly filled, ensuring efficient canopy coverage compared to areas with lower species asynchrony [9]. Consequently, it is evident that species asynchrony plays a pivotal role in fortifying community biomass stability in natural forests [5]. Our findings showed a noteworthy positive relationship between species asynchrony and both the μ and σ, exerting a substantial influence on the stability of community biomass, notably through the amplification of the mean biomass (μ). This indicated that highly diverse evergreen broadleaved forests possess an increased ability to promptly respond to local disturbances, thereby enhancing biomass stability. Additionally, the pivotal role of species asynchrony in adapting to changing environmental conditions by alleviating interspecific competition and habitat variability was underscored, resulting in an escalation of tree biomass within a specific range [4].

Recent research highlights the crucial importance of large trees, defined as those accounting for over 1% of the total biomass of a forest stand, in AGB stock, growth, and loss, surpassing even plant diversity and functional traits [5, 26]. The enhanced light-capturing abilities of large trees significantly contribute to species asynchrony by efficiently utilizing available light [20]. Some researchers have suggested that species asynchrony promotes temporal complementarity among species, thereby enhancing stability by reducing the variability (σ) of ecosystem functions [10]. However, it is noted that the impact of species asynchrony may sometimes diminish due to the slow response of trees to environmental changes in forest ecosystems [6].

Yu et al. suggested that further examination utilizing periodically collected data would clarify the potent influence of tree species asynchrony in driving community biomass stability and ensuring resilience within short temporal scopes [19]. This perspective underscores that the varied impacts of species asynchrony on stability depend on the temporal scale of analysis and the specific forest type. While the importance of species asynchrony in stabilizing ecosystem characteristics is widely recognized, there remains a lack of universally established empirical evidence within forest communities [5]. These findings suggest the necessity for future research to examine the effects of species asynchrony on stability across different natural forest types and temporal scales.

4.3. Stability of dominant species as the primary factor influencing community biomass stability

Our results have highlighted the pivotal role of stability in dominant species in shaping community biomass stability, surpassing the influence of species asynchrony. This corroborates previous research findings [27, 28]. In instances where biomass distribution is equitable among species, compositional effects are especially pronounced, particularly in communities with high species evenness [23]. Conversely, when a few dominant species govern the community, the temporal fluctuations of these species become the primary driver of biomass stability [23, 26]. This is because evenness tends to respond more swiftly to environmental changes compared to other ecological attributes like species richness, potentially leading to expedited ecosystem functionality responses [29]. Additionally, fluctuations in population stability under varying environmental conditions may directly impact community-level stability, particularly in scenarios where dominance is concentrated within a few species [8].

Due to the extended time required for woody species biomass production, changes in species composition within forest ecosystems tend to occur at a slow pace, reducing the significance of species asynchrony as a factor that promotes stability [9]. Typically, dominant species exert the most influence in forest communities, being both common and abundant [30]. They directly impact the community's structure, diversity, and biomass by affecting the occurrence, size, distribution, or abundance of other plant species. According to the mass-ratio hypothesis, dominant species may diminish the impact of species diversity on biomass, thereby directly influencing community biomass stability [7]. They often constitute a larger proportion of the large trees in forest stands and typically possess larger leaf area indices, enabling them to intercept more light and store more carbon through photosynthesis [26]. Additionally, small-scale spatial variations in net biomass heavily depend on biomass losses resulting from the mortality of large, mature trees [5]. Furthermore, the response of dominant species to climate change and soil conditions could have implications for the distribution, abundance, and dominance of remaining species in natural forests. It is also acknowledged that dominant species play a crucial role in moderating the influence of biodiversity on ecosystem functions [3]. Consequently, in our study, the stability of dominant species emerges as the primary determinant of community stability, surpassing factors such as biodiversity, stand structure, or species asynchrony.

4.4. Study limitations and implications

Chase et al. conducted a comprehensive examination of ecological drivers and their impact on biodiversity dynamics [31]. Their study unveiled a significant dependence on spatial scales in shaping these dynamics, illustrating how changes in taxonomic and functional diversity vary across different spatial scales. These findings illuminate the intricate relationship between biodiversity and spatial factors, underscoring the importance of considering spatial variables when assessing biodiversity responses to ecological drivers. Building on this perspective, Yu et al. further stressed the critical role of temporal stability in forest ecosystem productivity and community biomass [19]. Recognizing the limitations of current forest resource survey data, they emphasized the necessity of prioritizing assessments of AGB temporal stability over productivity. Their methodology necessitates rigorous data replication across sufficiently large plots to minimize errors, typically involving at least four repetitions of forest survey data [19]. Furthermore, the role of AGB as a crucial indicator of natural forest productivity has emerged, highlighting a consistent positive correlation with productivity across various spatial scales. Despite these findings, further exploration is needed to fully understand the complex pathways associated with the temporal stability of forest productivity [5].

Our study investigated the factors influencing the temporal stability of AGB in the evergreen broadleaved forest of Dong Nai Culture and Nature Reserve. Our findings reveal that factors such as overyielding, structural diversity, species asynchrony, and the stability of dominant species exert significant influence on community biomass stability. Particularly noteworthy is the substantial impact of quality effects over quantity effects in evergreen broadleaved forests. This underscores the intricate interplay of factors that govern the temporal stability of AGB within this forest type.

Effective forest management strategies are crucial for enhancing the health and productivity of forest ecosystems, necessitating a comprehensive and adaptive approach. This approach involves considerations of species richness, stand structure, species asynchrony, and the stability of dominant species [14, 22]. Based on our findings, we propose specific recommendations: Firstly, our study identified a negative correlation between species richness and both μ and σ, suggesting that increasing species diversity does not necessarily lead to stabilized forest biomass over time. Therefore, forest management efforts should prioritize biodiversity conservation to bolster ecosystem resilience, while also considering factors such as forest stand structure and species asynchrony. Secondly, the higher coefficient of variation in DBH showed a negative association with both μ and σ, indicating that forests with more uniform age and size distributions may exhibit less stability. Management practices should aim to diversify tree age and size structures to enhance forest stability. Thirdly, positive correlations between species asynchrony and community biomass stability, and between mean biomass and biomass variability, indicate that forests with non-synchronized species growth and decline phases achieve better overall stability. Therefore, management strategies should promote diverse species with varying growth rates and peak biomass times to improve forest resilience. Lastly, the strong positive correlation between the stability of dominant species and overall community biomass stability underscores the critical role of maintaining the health and stability of key species in ecosystem balance. Hence, protecting and promoting conditions favorable to dominant species is essential for sustaining forest ecosystems in the study area.

5. CONCLUSION

In this study, we found that the impact of overyielding on the biomass stability of evergreen broadleaved forests was considered negligible. Instead, our findings revealed that species richness exerts its influence indirectly through alternative mechanisms, while the significance of forest structure surpasses that of overyielding. Our study highlighted that while the stability of dominant tree species and species asynchrony significantly affect the biomass stability of forest stands, the stability of dominant species emerges as the primary direct influencer of community biomass stability. We emphasized the pivotal role of dominant tree species in maintaining forest ecosystem stability, prioritizing them over species asynchrony or overyielding. This finding aligns with our study's support for the mass-ratio hypothesis, which suggests that the functional trait composition or the dominant species primarily determines ecosystem function.

Our results will lay the groundwork for developing strategies to enhance the stability of evergreen broadleaved forests in Vietnam. Furthermore, our exploration of the relationships between various mechanisms and community biomass stability underscores their complexity and diversity. This complexity likely arises from variations in the definitions of mechanisms and stability and differences in temporal and spatial scales, forest types, stages of forest succession, and ecological disturbances.

Therefore, delving into more precise and comprehensive mechanisms across diverse research landscapes in future endeavors is crucial. This approach will enable a deeper understanding of the factors influencing tropical forest ecosystem stability and facilitate the development of targeted conservation and management strategies.

In conserving species diversity and ensuring the sustainability of natural resources, scientific research in nature conservation and ecosystem management focuses primarily on preserving stability within animal and plant communities, alongside investigating mechanisms that regulate community stability. Rutherford classified science into two categories: genuine science (physics) and what he referred to as "stamp collecting" [32]. Our study unequivocally demonstrates that our research surpasses mere inquiry—it constitutes valuable reference material on tropical forest dynamics in theoretical ecology.

REFERENCES

[1]. Hartmann H., Bastos A., Das A. J., Esquivel-Muelbert A., Hammond W. M., Martínez-Vilalta J., McDowell N. G., Powers J. S., Pugh T. A. & Ruthrof K. X. (2022). Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annual Review of Plant Biology. 73: 673-702.

[2]. Funk J. M., Aguilar-Amuchastegui N., Baldwin-Cantello W., Busch J., Chuvasov E., Evans T., Griffin B., Harris N., Ferreira M. N. & Petersen K. (2019). Securing the climate benefits of stable forests. Climate Policy. 19(7): 845-860.

[3]. Gross N., Suding K., Lavorel S. & Roumet C. (2007). Complementarity as a mechanism of coexistence between functional groups of grasses. Journal of Ecology. 95(6): 1296-1305.

[4]. Loreau M., Barbier M., Filotas E., Gravel D., Isbell F., Miller S. J., Montoya J. M., Wang S., Aussenac R. & Germain R. (2021). Biodiversity as insurance: from concept to measurement and application. Biological Reviews. 96(5): 2333-2354.

[5]. Zhou T., Zhang J., Qin Y., Zhou G., Wang C., Xu Y., Fei Y., Qiao X. & Jiang M. (2023). Species asynchrony and large trees jointly drive community stability in a montane subtropical forest. Ecosystems. 26(4): 740-751.

[6]. Craven D., Eisenhauer N., Pearse W. D., Hautier Y., Isbell F., Roscher C., Bahn M., Beierkuhnlein C., Bönisch G. & Buchmann N. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. Nature ecology & evolution. 2(10): 1579-1587.

[7]. Grime J. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology. 86(6): 902-910.

[8]. Hallett L. M., Hsu J. S., Cleland E. E., Collins S. L., Dickson T. L., Farrer E. C., Gherardi L. A., Gross K. L., Hobbs R. J. & Turnbull L. (2014). Biotic mechanisms of community

stability shift along a precipitation gradient. Ecology. 95(6): 1693-1700.

[9]. Ma F., Zhang F., Quan Q., Song B., Wang J., Zhou Q. & Niu S. (2021). Common species stability and species asynchrony rather than richness determine ecosystem stability under nitrogen enrichment. Ecosystems. 24: 686-698.

[10]. Wagg C., Roscher C., Weigelt A., Vogel A., Ebeling A., De Luca E., Roeder A., Kleinspehn C., Temperton V. M. & Meyer S. T. (2022). Biodiversity–stability relationships strengthen over time in a long-term grassland experiment. Nature Communications. 13(1): 7752.

[11]. Jenkins M. & Schaap B. (2018). Forest ecosystem services. Background analytical study. 1.

[12]. Shi Z., Xu X., Souza L., Wilcox K., Jiang L., Liang J., Xia J., García-Palacios P. & Luo Y. (2016). Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. Nature communications. 7(1): 11973.

[13]. Schnabel F., Schwarz J. A., Dănescu A., Fichtner A., Nock C. A., Bauhus J. & Potvin C. (2019). Drivers of productivity and its temporal stability in a tropical tree diversity experiment. Global change biology. 25(12): 4257-4272.

[14]. Ouyang S., Xiang W., Gou M., Chen L., Lei P., Xiao W., Deng X., Zeng L., Li J. & Zhang T. (2021). Stability in subtropical forests: The role of tree species diversity, stand structure, environmental and socio‐economic conditions. Global Ecology and Biogeography. 30(2): 500-513.

[15]. Nguyen Van Quy, Vu Manh, Nguyen Van Hop, Nguyen Van Lam, Nguyen Van Thanh & Nguyen Hong Hai (2023). Niche and interspecific association of tree species in an evergreen broadleaved forest in Dong Nai Culture and Nature Reserve. Vietnam Journal of Forest Science. 5: 84-101.

[16]. Pham Hoang Ho (1999-2003). An Illustrated Flora of Vietnam. ed. Vol. 1-3. Young Publishing House. Hanoi, Vietnam.

[17]. Tran Hop (2002). Timber trees resources in Vietnam. ed. Agricultural Publishing House. Hanoi, Vietnam.

[18]. Chave J., Réjou‐Méchain M., Búrquez A., Chidumayo E., Colgan M. S., Delitti W. B., Duque A., Eid T., Fearnside P. M. & Goodman R. C. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. Global change biology. 20(10). 3177-3190.

[19]. Yu S. J., Wang J., Zhang C. Y. & Zhao X. H. (2022). Impact and mechanism of maintaining biomass stability in a temperate coniferous and broadleaved mixed forest. Chinese Journal of Plant Ecology. 46(6): 632.

[20]. Forrester D. I. (2019). Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. Forest Ecology and Management. 447: 139-157.

[21]. Forrester D. I., Rodenfels P., Haase J., Härdtle W., Leppert K. N., Niklaus P. A., von Oheimb G., Scherer-Lorenzen M. & Bauhus J. (2019). Tree-species interactions increase light absorption and growth in Chinese subtropical mixed-species plantations. Oecologia. 191: 421-432.

[22]. Petchey O. L., Casey T., Jiang L., McPhearson P. T. & Price J. (2002). Species richness, environmental fluctuations, and temporal change in total community biomass. Oikos. 99(2): 231-240.

[23]. Gross K., Cardinale B. J., Fox J. W., Gonzalez A., Loreau M., Wayne Polley H., Reich P. B. & van Ruijven J. (2014). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. The American Naturalist. 183(1): 1-12.

[24]. Valencia E., De Bello F., Galland T., Adler P. B., Lepš J., E-Vojtkó A., van Klink R., Carmona C. P., Danihelka J. & Dengler J. (2020). Synchrony matters more than species richness in plant community stability at a global scale. Proceedings of the National Academy of Sciences. 117(39): 24345-24351.

[25]. Yuan Z., Ali A., Wang S., Wang X., Lin F., Wang Y., Fang S., Hao Z., Loreau M. & Jiang L. (2019). Temporal stability of aboveground biomass is governed by species asynchrony in temperate forests. Ecological indicators. 107: 105661.

[26]. Ali A., Lin S. L., He J. K., Kong F. M., Yu J. H. & Jiang H. S. (2019). Big‐sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. Global Change Biology. 25(8): 2810-2824.

[27]. Li X., Zuo X., Qiao J., Hu Y., Wang S., Yue P., Cheng H., Song Z., Chen M. & Hautier Y. (2024). Context‐dependent impact of changes in precipitation on the stability of grassland biomass. Functional Ecology.

[28]. Hou G., Zhou T., Shi P., Sun J., Zong N., Yu J. & Song M. (2023). Multi-year nitrogen accumulation weakens the stabilizing effect of species asynchrony on drought resistance in a Tibetan alpine meadow. Agricultural and Forest Meteorology. 340: 109617.

[29]. Xu Z., Ren H., Li M. H., van Ruijven J., Han X., Wan S., Li H., Yu Q., Jiang Y. & Jiang L. (2015). Environmental changes drive the temporal stability of semi‐arid natural grasslands through altering species asynchrony. Journal of Ecology. 103(5): 1308-1316.

[30]. Avolio M. L., Forrestel E. J., Chang C. C., La Pierre K. J., Burghardt K. T. & Smith M. D. (2019). Demystifying dominant species. New Phytologist. 223(3): 1106-1126.

[31]. Chase J. M., McGill B. J., McGlinn D. J., May F., Blowes S. A., Xiao X., Knight T. M., Purschke O. & Gotelli N. J. (2018). Embracing scale‐dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecology letters. 21(11): 1737-1751.

[32]. Satoo T. & Madgwick H. (2012). Forest biomass. ed. Vol. 6. Springer Science & Business Media.