

Research article

Linking forest coverage and fragmentation to the dark diversity of plant communities under different forest management practices



Ji-Zhong Wan *, Xiaodan Wang *

Key Laboratory of Mountain Surface Processes and Ecological Regulation, Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, Chengdu, China

ARTICLE INFO

Keywords:

Biodiversity indicator
Community completeness
Forest management
General linear mixed model
Observed diversity
Plantation forests

ABSTRACT

Dark diversity refers to species that belong to a particular species pool, although they are locally absent from the given sites. To understand the effects of forest coverage and fragmentation on plant species diversity, we examined whether coverage and fragmentation influence the dark diversity of plant communities in forests under different management practices. We compiled a comprehensive database to quantify the observed diversity, dark diversity, and community completeness of managed forests. We used regression models with forest management practice type as a random factor to determine the relationships among observed diversity, dark diversity, and community completeness with forest coverage and fragmentation. We detected significant associations between forest coverage and fragmentation and the observed diversity, dark diversity, and community completeness of forests, although these associations tended to be weak on a global scale. Forest management practices play a crucial role in determining the effects of forest coverage and fragmentation on dark diversity, offering valuable insights into biodiversity conservation and ecological restoration management. Increased forest coverage initially declined and subsequently increased the observed diversity and community completeness in tropical plantation forests (rotation ≤ 15 years) in both 2000 and 2020. Conversely, in both assessed years, the increasing forest fragmentation tended to result in initially increasing and then decreasing observed diversity, dark diversity and community completeness in tropical plantation forests (rotation ≤ 15 years). Forest fragmentation had a positive effect on the dark diversity in temperate plantation forests (rotation > 15 years). The contrasting effects of forest fragmentation on dark diversity between tropical plantation forests (with rotation ≤ 15 years) and temperate planted forests (with rotation > 15 years) have different management implications for the conservation and restoration of plant diversity. Consequently, dark diversity and community completeness can be used to predict changing trends in species diversity of plant communities, using forest coverage and fragmentation as direct indicators and measures for biodiversity conservation and environmental management, depending on the type of biome and rotation time.

1. Introduction

Forests provide multiple ecosystem functions and services, including the production of tree biomass; carbon storage; the production of berries, mushrooms, and game; and recreational potential (Brokerhoff et al., 2017; Mori et al., 2017). Forest fragmentation, which is associated with a reduction in patch size, an increase in patch number, and larger extents of forest edges, is a landscape-level process that contributes to the loss of plant species diversity and declines in ecosystem functions and services (Cousins et al., 2007; Mitchell et al., 2014; Ma et al., 2023). Therefore, effective tools are required to address the loss of species diversity and ecosystem integrity. Comprehensive quantification of global

forest fragmentation is an effective tool for guiding forest protection, restoration, and reforestation policies (Ma et al., 2023), and numerous studies have examined the effects of forest coverage and fragmentation on the diversity of plant communities (Cousins et al., 2007; Liebsch et al., 2021; Ramirez-Delgado et al., 2022; Ma et al., 2023). However, few studies have assessed the association between forest coverage, fragmentation, and dark diversity in forest plant communities.

We used the concept of dark diversity (which refers to a set of species that are absent from a given site, although present in the surrounding regions and can potentially inhabit the site) to gain a better understanding of the effects of forest fragmentation on plant species diversity (Pärtel et al., 2011; Moeslund et al., 2017; Riibak et al., 2024). Dark

* Corresponding author.

E-mail address: wxd@imde.ac.cn (X. Wang).

diversity is a taxon-oriented concept that considers the suitability of a particular site for each absent species (Ronk et al., 2015; Lewis et al., 2017). Both observed and dark diversities constitute a site-specific species pool, which includes only species from regions suitable for a given site under ecological processes (Pärtel et al., 2011). Typically, slow evolutionary and biogeographical processes, such as speciation and changes in distributional ranges, dominate species pools at regional and continental scales, whereas at local scales, more rapid ecological processes, such as forest fragmentation and human activities, tend to have a more pronounced influence on the observed diversity of plant species (Carstensen et al., 2013; De Bello et al., 2016; Schlüter and Pennell, 2017; Trindade et al., 2020). Furthermore, we used observed and dark diversities to assess the completeness of plant communities in the forests. In this regard, community completeness can be quantified using the log ratio of observed and dark diversities, thereby suggesting the proportion of the species pool within a local community (Pärtel et al., 2013; Noreika et al., 2020) and facilitating the comparison of local biodiversity among regions, ecosystems, and taxonomic groups at different spatial scales (Pärtel et al., 2013; Riibak et al., 2015; Bennett et al., 2016).

Forest management practices are closely associated with the conservation of biodiversity, ecological restoration, sustainable forest management, and ecosystem maintenance (Lesiv et al., 2022). We assessed changes in observed species diversity in response to various management practices, highlighting the role of forest management practices in conserving plant species diversity in the context of forest fragmentation. Plant species diversity is influenced by natural conditions, particularly by climate and human disturbance (Thuiller et al., 2005; Bell et al., 2016), and recently, human-induced forest loss and fragmentation have been shown to have detrimental effects in terms of plant species diversity (Ma et al., 2023; Arnesi et al., 2024). The decline in the diversity of plant species can have adverse impacts on the function and stability of entire ecosystems (Führer, 2000). Consequently, a greater understanding of the patterns and mechanisms of plant species diversity may contribute to the conservation of forest ecosystems. The direct detrimental effects of anthropogenic activities, involving forest management practices, may be important for assessing plant species diversity, and sound knowledge of dark diversity can contribute to determining whether forest fragmentation drives dark diversity in plant communities in response to changes in forest management types (Pärtel et al., 2013, 2025).

Dark diversity has implications for biodiversity conservation and ecological restoration under forest management practices (Pärtel et al., 2013; Riibak et al., 2020). Numerous studies (e.g., Mori et al., 2017; Nguon and Kulakowski, 2013; Mitchell et al., 2014; Zhang et al., 2024) have assessed the effectiveness of forest management practices on observed species diversity, ranging from community to global scales, guiding policies and decision-making on ecosystem functions and services such as forest conservation, renewable energy, potential supply assessment of forest biomass, carbon accounting, and forest restoration practices. However, with global threats, the observation of species diversity may be changed due to different spatial and temporal scales (e.g., the changes in spatial scale, and legacy effects); therefore, there is a high possibility that forest management effectiveness may be reduced (Liebsch et al., 2021; Ma et al., 2023; Wan and Wang, 2023; Pärtel et al., 2025). The dark diversity framework can contribute to a growing recognition that biodiversity assessments should move beyond presence-based metrics and incorporate the latent ecological potential of communities to offer important implications for conservation planning and ecological restoration. Based on the links of forest coverage and fragmentation to the dark diversity of plant communities, effective models should be developed to predict the changing trends of plant community diversity under different forest management practices. Hence, it is reasonable to assume that a better understanding of forest management practices can be achieved by combining assessment of observed diversity, dark diversity, and community completeness rather

than focusing solely on observed diversity under forest coverage and fragmentation.

The main objective of this study was to determine whether dark diversity in plant communities is associated with forest coverage and fragmentation. We proposed the following two hypotheses: (H1) significant associations exist between forest coverage and fragmentation and dark diversity, and (H2) the effects of forest coverage and fragmentation on dark diversity may differ depending on differences in the type of forest management. Accordingly, we sought to determine the effects of different types of forest management on dark diversity, which has a pronounced influence on forest coverage and fragmentation and could provide a basis for ecological management for the conservation and restoration of forests. We compiled a comprehensive dataset of plots from various sources. Using this dataset, we applied regression models to assess the associations between observed and dark diversities and forest coverage and fragmentation on a global scale, with the type of forest management practice serving as a random factor.

2. Materials and methods

2.1. Plot data

Plot data for species composition were obtained from the sPlotOpen database v2.1 (Sabatini et al., 2021; <https://doi.org/10.25829/1div.3474-40-3292>), the BIEN database (version 4.2; Maitner et al., 2018), studies conducted by Jeliazkov et al. (2020), Jin et al. (2022), and Wang et al. (2023, 2024), and our fieldwork in Tianshui and adjacent areas in Gansu Province, China (Fig. 1). We obtained a global map of the 14 biomes from Dinerstein (2017), and based on the studies performed by these authors, we used a global map of 867 ecoregions within the 14 biomes as a basis for identifying conservation measures and ecological processes. Forest ecoregions are generally characterized by similar patterns of species accumulation and community similarity to improve their potential application in conservation efforts under environmental management (Smith et al., 2018). Hence, forest ecoregions are an effective tool for monitoring biodiversity trends and assessing the effectiveness of conservation management. In the current study, we used terrestrial biomes (which are large land areas with geographically distinct assemblages of plant communities and environmental conditions; Dinerstein et al., 2017). The study area comprises six forest biomes: tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, tropical and subtropical coniferous forests, temperate broadleaf and mixed forests, temperate conifer forests, and boreal forests/taiga. The plot distribution overlapped the latest shape file map of forest ecoregions reported by Dinerstein et al., 2017; <https://ecoregions.appspot.com/>), which were classified as temperate or tropical.

We checked the scientific names of the plant species based on a study conducted by Brown et al. (2023). We evaluated the species data of the plots using a quality control workflow based on geographic coordinates, duplications, native ranges, and geographical and environmental outliers, rating each occurrence data point from AAA (i.e., high geographic precision and low environmental uncertainty) to E (i.e., missing coordinates). Following Serra-Díaz et al. (2017), we selected only high-quality species occurrence data within plots for our analyses, which were labeled AAA, AA, A, and C with no B. Finally, we removed plot data that were not covered by the studied forest ecoregions and were not distributed in native ranges.

Plot maps with more than 25 records of species composition per plot were produced for 158 ecoregions, and matrices were constructed for species plots within each ecoregion to measure diversity. Among all the plots, we obtained abundance data for each species, and within each specific forest ecoregion, pairwise co-occurrence was examined using the abundance data for each species and plot. Plots with fewer than three observed plant species were excluded from the analysis, given the low confidence interval of the plot data. Finally, the study plots were

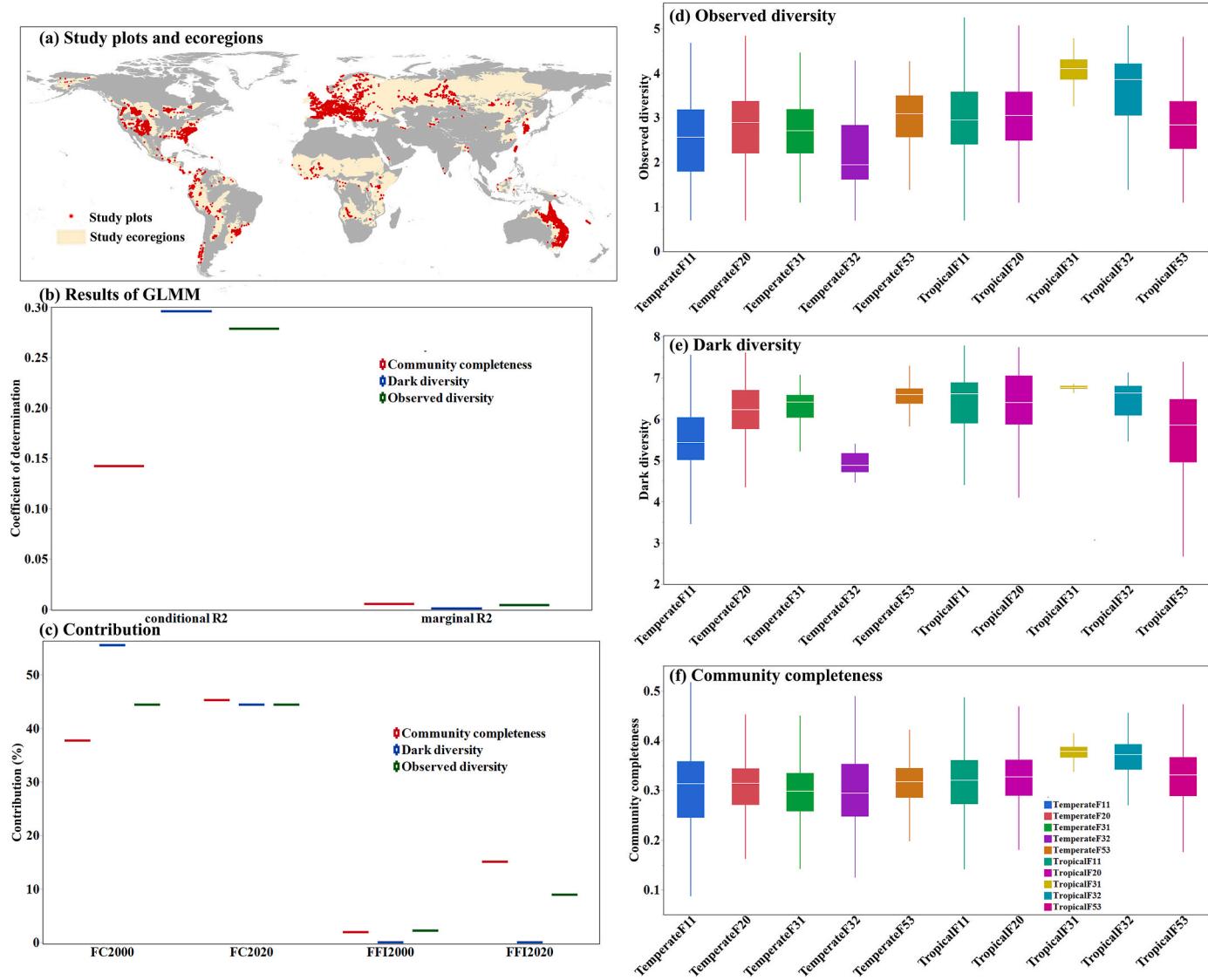


Fig. 1. (a) Distribution map of study plots and ecoregions. (b) The marginal and conditional coefficient of determination (marginal R^2 and conditional R^2) of GLMM for associations between three diversity matrices (i.e., observed diversity, dark diversity, and community completeness) and forest coverage and fragmentation in 2000 and 2020. (c) The boxplots of three diversity matrices across different types of forest management practices in 2000 and 2020. (d, e, and f). FC represents forest coverage and FFI represents forest fragmentation index. In panels b and c, the results are shown as observed diversity (green), dark diversity (blue), and community completeness (red). The differences among the means of observed diversity, dark diversity, and community completeness among different forest management practices; all the pairs between two forest management practices were significant based on Tukey's HSD test ($P < 0.1$). Boxplots represent the median (center line), interquartile range (boxes), and full range (whiskers).

subjected to different forest management practices. The total number of study plots was 41,081, and the plant species in each study plot were investigated within a minimum area of 10×10 m, closely consistent with the study by Pärtel et al. (2025).

2.2. Data on forest management practices

For forest management, we obtained data on forest management practices up until February 2019, as represented by Lesiv et al. (2022). Consistent with these studies, we classified the types of forest management into the following five groups: (F11) naturally regenerating forests without any signs of management, (F20) naturally regenerating forests with signs of forest management, (F31) planted forests (rotation >15 years), (F32) plantation forests (rotation ≤ 15 years), (F40) oil palm plantations, and (F53) agroforestry. These management types are based on the observed level of human impact and length of rotation, which are distinguishable from the visual interpretations of satellite imagery

(Lesiv et al., 2022). To reduce these effects, the level of human impact and the rotation time observed in forest management practices are linked to the rate of forest disturbance. Based on a study by Lesiv et al. (2022), we used 226,322 unique locations at a $100 \text{ m} \times 100 \text{ m}$ resolution using Geo-Wiki (<https://www.geo-o.org/>), an online application used for crowdsourcing, and engaged with the assistance of an expert in the visual interpretation of satellite imagery. The location dataset represents the status of forest ecosystems and can be used to investigate the value of forests in terms of species, ecosystems, and services (Lesiv et al., 2022). In this study, we defined five temperate and five tropical forest management practices based on their overlap with temperate and tropical ecoregions.

2.3. Data on forest coverage and fragmentation

Data on forest coverage and fragmentation were obtained from a study conducted by Ma et al. (2023). Ma et al. (2023) produced global

distribution maps of forest coverage and fragmentation based on the main characteristics of forest fragmentation, including edge, isolation, and patch size effects. The 30 m forest coverage data were processed to produce binary forest maps for 2000 and 2020, and these maps were used to calculate three fragmentation-related landscape metrics (edge density, patch density, and mean patch area) at a grid cell resolution of 5000×5000 m for each of these years. To generate maps of forest coverage for 2000 and 2020 at a grid cell resolution of 5000×5000 m, we used a 5000-m grid to calculate forest coverage, namely, the percentage of forest area to total area in a specific grid cell.

As shown by Pärtel et al. (2025), large spatial scales of human footprints coupled with forest coverage affect dark diversity assessments. To model the ecological process of dark diversity that is ecologically suitable and present in a region but currently absent from a given site, we restrained the study site to a grid cell resolution of 5000 m \times 5000 m, which is much smaller than the 200 km shown in the study by Pärtel et al. (2025). In the current study, we used a synthetic forest coverage and fragmentation index to examine the impact of forest fragmentation on observed diversity, dark diversity, and community completeness at a scale of 5000 m \times 5000 m for each site. Based on a rotation time of less than or more than 15 years, as shown in a study by Lesiv et al. (2022), the period between 2000 and 2020 should be considered to quantify the effects of forest management practices on tree species diversity at temporal scales. We collected the sampling data two times to enhance the robustness of the study. This study assessed how forest coverage and fragmentation affect the observed diversity, dark diversity, and community completeness, which could enhance the effectiveness of forest management across spatial and temporal scales.

2.4. Diversity measures

Plant community species diversity was assessed based on abundance data, for which species \times plot matrices were produced. Observed diversity was assessed based on the number of plant species (Pärtel et al., 2013), whereas dark diversity was quantified by considering similar environmental backgrounds within each ecoregion; estimates for each ecoregion were obtained using the hypergeometric method based on pairwise associations between species using species \times species co-occurrence matrices (Carmona and Pärtel, 2021). Based on the hypergeometric method, for each pair of species, we can compare the realized number of co-occurrences with random expectations (i.e., if there is no association between species; Carmona and Pärtel, 2021). The probability distribution of the hypergeometric method encompasses the entire range of available probabilities (Carmona and Pärtel, 2021). The hypergeometric method is currently a flexible and robust method with the best modeling performance for estimating probabilistic dark diversity and species pool composition based on pairwise species co-occurrence (Carmona and Pärtel, 2021; Chollet et al., 2025; Pärtel et al., 2025).

Based on an established co-occurrence methodology (Carmona and Pärtel, 2021), we adopted a stacking approach in which all species occurring in a region but absent from the focal site were assigned a probability of inclusion in the dark diversity. Dark diversity was assessed based on the sum of the probabilities of absent species ranging from 0 to 1 in each plot (Carmona and Pärtel, 2021; Pärtel et al., 2025). Community completeness was computed as the percentage of observed diversity among all suitable species (i.e., observed and dark diversities) at a given site (Pärtel et al., 2013; Carmona and Pärtel, 2021). To estimate the dark diversity within a specific ecoregion, we used the 'DarkDiv' package in the R environment (<https://www.r-project.org/>) to calculate the probability of a species occurring in a plot based on its co-occurrence with other species.

2.5. Analysis

Tukey's HSD test was used to analyze the differences among the

means of observed diversity, dark diversity, and community completeness with respect to different forest management practices. To examine the associations between forest coverage and fragmentation and the observed diversity, dark diversity, and community completeness on a global scale for 2000 and 2020 (assessed based on marginal and conditional coefficients of determination [R^2]), we used general linear mixed models (GLMMs), with the type of forest management practice used as a random factor (Lai et al., 2022). Global patterns were assessed using the entire dataset. In this context, a large difference between the marginal R^2 and conditional R^2 values suggests that forest management practices could contribute to the observed diversity, dark diversity, and community completeness.

Linear and second-order polynomial regression models were used to account for the relationships observed between forest coverage and fragmentation in 2000 and 2020 and the raw data on observed diversity, dark diversity, and community completeness at the scale of forest management practices, relying solely on diversity matrices and forest variables. The analysis was conducted using a dataset based on each forest management practice, and the coefficient of determination (R^2) was used to quantify the effects of forest coverage and fragmentation on observed diversity, dark diversity, and community completeness. We compared the R^2 values between the linear and second-order polynomial regression models and used the models with higher R^2 values for further analyses. All analyses were conducted using R (<https://www.r-project.org/>) and JMP 17.0 (https://www.jmp.com/zh_cn/home.html).

3. Results

The observed diversity, dark diversity, and community completeness differed significantly among the sites subjected to different forest management practices (Fig. 1). The observed diversity was highest in tropical planted forests (rotation >15 years; Fig. 1), whereas dark diversity and community completeness were the highest in tropical planted forests (rotation >15 years) and temperate agroforests (Fig. 1). Tropically planted forests (rotation >15 years) accounted for the largest area of forest coverage, and naturally regenerating forests with signs of forest management were the most fragmented in 2000 and 2020 (Table S1). Although the results of the GLMM revealed significant associations between forest coverage and fragmentation and observed diversity, dark diversity, and community completeness (Fig. 1), these relationships tended to be relatively weak on a global scale (Fig. 1). Moreover, there were large differences in the values obtained for marginal R^2 and conditional R^2 , indicating that forest management type played an important role in the effects of forest coverage and fragmentation on diversity indices (Fig. 1). Furthermore, for different forest management practices on a global scale, the effects of forest coverage and fragmentation on dark diversity and community completeness were stronger in 2020 than in 2000 (Fig. 1), and forest coverage in 2020 was significantly associated with the diversity observed in naturally regenerating temperate forests without any signs of management (Table S2).

The values of R^2 were lower based on the linear than second-order polynomial regression models, so we described the results based on the second-order polynomial regression models (Table S3). In both 2000 and 2020, forest fragmentation was shown to have strong associations with dark diversity in tropical plantation forests (rotation \leq 15 years) and temperate planted forests (rotation of >15 years) (Fig. 2). In addition, we detected strong associations between forest coverage and fragmentation and observed diversity and community completeness in tropical plantation forests (rotation \leq 15 years) (Fig. 2). Similarly, in both assessed years, we obtained evidence for the strong effect of forest coverage on dark diversity in tropical plantation forests (rotation \leq 15 years), although the effects in temperate planted forests (rotation of >15 years) tended to be comparatively weak (Fig. 2).

In both 2000 and 2020, the association between dark diversity and forest coverage in tropical plantation forests (rotation \leq 15 years) initially increased and then declined (Fig. 3). However, the association

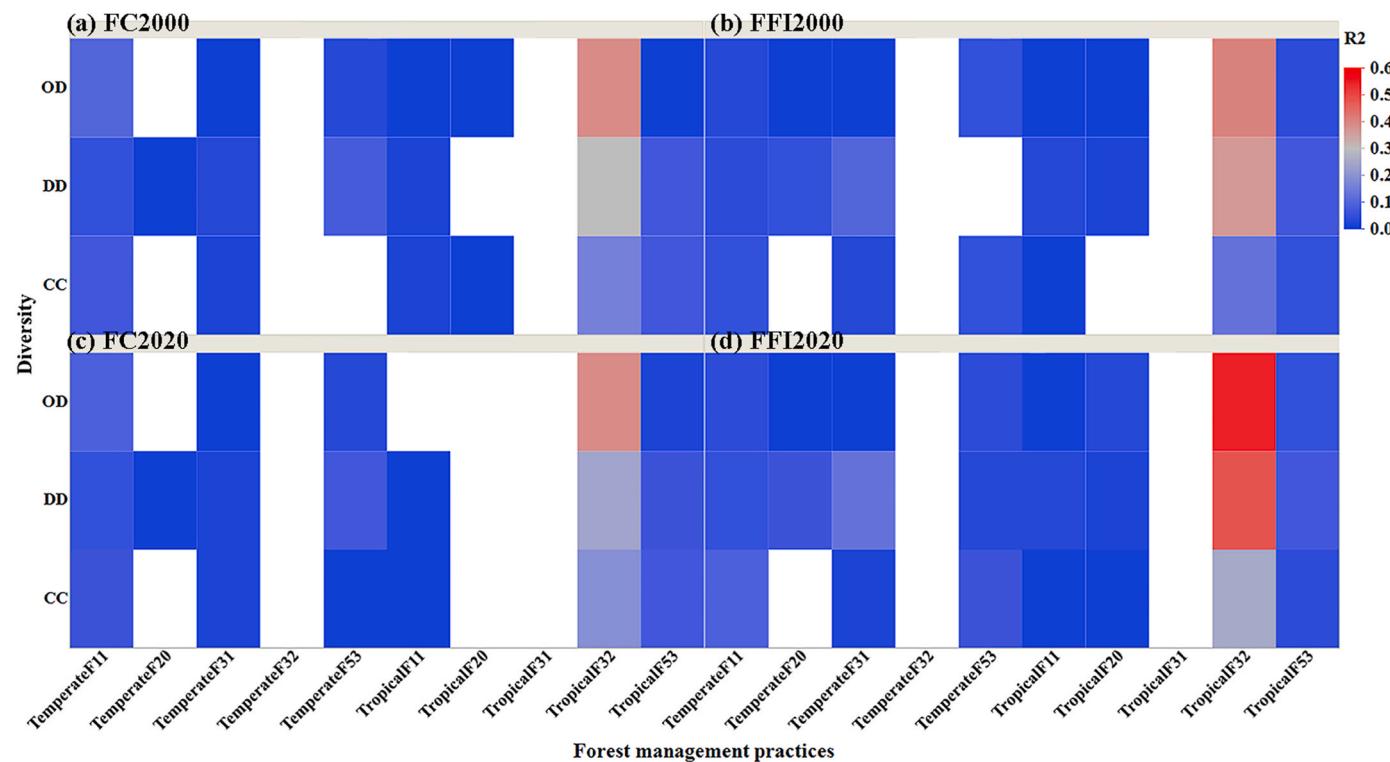


Fig. 2. Coefficient of determination (R^2) of the second-order polynomials for the associations between diversity matrices [i.e., observed diversity (OD), dark diversity (DD), and community completeness (CC)] and forest coverage and fragmentation among different forest management practices in 2000 and 2020. All relationships were significant ($P < 0.1$) with color grids. The colors from blue to red represent an increase in values of R^2 . The codes of forest management practices are as follows: (F11) naturally regenerating forests without any signs of management, (F20) naturally regenerating forests with signs of forest management, (F31) planted forests (rotation >15 years), (F32) plantation forests (rotation ≤ 15 years), and (F53) agroforestry. FC represents forest coverage and FFI represents forest fragmentation index.

between dark diversity and forest coverage was weak in temperate plantation forests (rotation >15 years; $R^2 = 0.02$ for 2000 and $R^2 = 0.03$ for 2020). The observed diversity ($R^2 = 0.39$ for 2000 and $R^2 = 0.39$ for 2020), and community completeness ($R^2 = 0.19$ for 2000 and $R^2 = 0.16$ for 2020) initially declined and subsequently increased with increasing forest coverage in tropical plantation forests (rotation ≤ 15 years; Fig. 4).

In both 2000 and 2020, forest fragmentation had a positive effect on the dark diversity in temperate plantation forests (rotation >15 years; $R^2 = 0.10$ for 2000; and $R^2 = 0.13$ for 2020; Fig. 3). Conversely, in both assessed years, the increasing forest fragmentation tended to result in the initially increasing and then decreasing observed diversity ($R^2 = 0.41$ for 2000 and $R^2 = 0.55$ for 2020), dark diversity ($R^2 = 0.37$ for 2000 and $R^2 = 0.48$ for 2020) and community completeness ($R^2 = 0.13$ for 2000 and $R^2 = 0.25$ for 2020) in tropical plantation forests (rotation ≤ 15 years; Figs. 3 and 4). Overall, we observed that forest fragmentation was positively associated with dark diversity, but such associations were the opposite for observed diversity and community completeness (Figs. 3 and 4).

4. Discussion

Our findings revealed associations between forest coverage and fragmentation and the dark diversity of plant communities within forests subjected to different management practices. However, on a global scale, these relationships were reported to depend on the type of forest management practice. Consequently, models based on forest management practices should be developed to predict species diversity of plant communities based on dark diversity. Observed diversity, dark diversity, and community completeness were the highest in tropical planted forests (rotation >15 years), indicating that observed and dark diversities could be enhanced with increasing rotation time of tropical forests,

which could be associated with an enhancement of observed diversity and community completeness due to a transition from dark diversity (Riibak et al., 2024). Our findings provide evidence of high-level dark diversity in tropical forests. Based on the concept of dark diversity, we would predict that with increasing rotation time, plantation forests will provide suitable habitats for a larger number of species within plant communities.

However, despite evidence that in both 2000 and 2020, forest coverage and fragmentation had significant effects on the observed diversity, dark diversity, and community completeness in tropical plantation forests (rotation ≤ 15 years), the effects of forest fragmentation on dark diversity and community completeness (also observed diversity) were the opposite for increasing and declining forest coverage intervals. During the primary succession of tropical plantation forests, forest fragmentation may be caused by pioneer species with a high probability of masking an area and increasing the number of patches (Zhu et al., 2004; Jakovac et al., 2021). Ecological niches support more potential species, resulting in high dark diversity during the primary succession of tropical plantation forests in response to increasing forest fragmentation (Pagel and Schurr, 2012; Sloan et al., 2016). Under dynamic equilibrium conditions, we observed an increase in species richness within plant communities, as reflected by high community completeness (Cramer and Verboom, 2024). The maximum number of species that can co-occur in a given assemblage at a certain point in time is determined by habitat conditions (carrying capacity) and the number of species available for the colonization of habitats in the late period of tropical plantation forests (rotation ≤ 15 years) (Storch and Okie, 2019). Forest fragmentation may lead to the fragmentation or reduction of suitable habitats, thereby resulting in smaller populations that are more susceptible to random extinction (Ramírez-Delgado et al., 2022; Zhang et al., 2024). In addition, habitat fragmentation and loss are likely to reduce

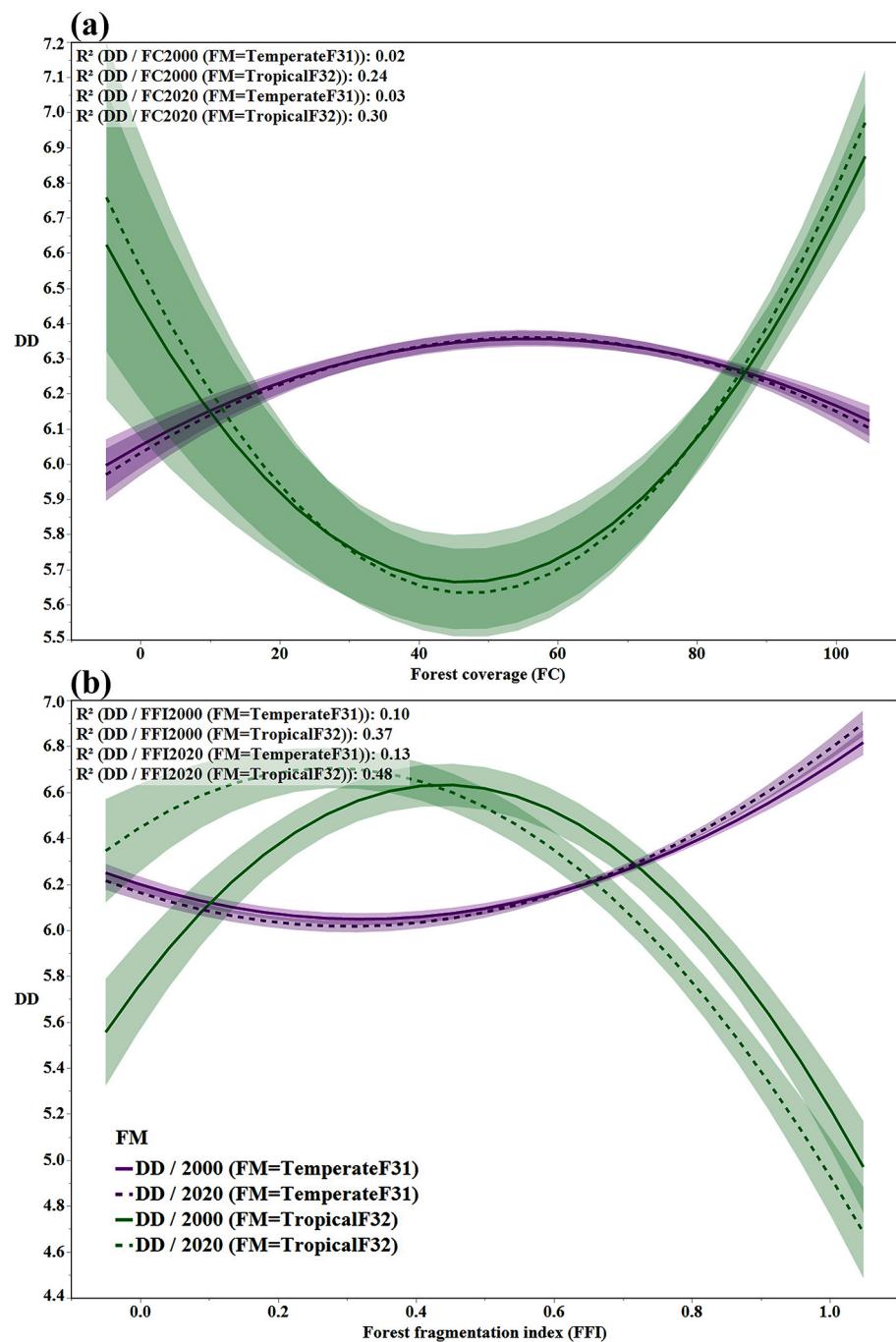


Fig. 3. Associations between dark diversity (DD) and forest coverage (FC) and fragmentation index (FFI) based on the second-order polynomial. The shaded band is a pointwise 95 % confidence interval on the fitted values. The solid and dashed lines represent the forest management practices in 2000 and 2020, respectively. All the relationships were significant at the $P < 0.1$ level.

connectivity among the remaining patches of natural vegetation, thereby resulting in the isolation of populations and increasing difficulty in species movement between areas of suitable habitats (Naaf et al., 2021; Ramírez-Delgado et al., 2022). Moreover, defaunation may disrupt plant seed-dispersal networks (Riibak et al., 2017). Consequently, fragmentation contributes to an overall decline in community completeness over time, which is associated with a decline in connectivity among patches and a weakening of co-occurrence patterns in old plant communities (Uroy et al., 2019; Calcagno et al., 2022). Hence, in plant communities within tropical plantation forests (rotation ≤ 15 years), low community completeness is assumed to be associated with a reduction in dark diversity.

We observed that increasing forest coverage initially declined and subsequently increased the observed diversity and community completeness in tropical plantation forests (rotation ≤ 15 years) in both 2000 and 2020. Furthermore, the association between dark diversity and forest coverage was weak. Hence, large forest coverage could enhance observed diversity and community completeness in tropical plantation forests (rotation ≤ 15 years). Therefore, high levels of forest coverage should remain in tropical forests with short rotation time

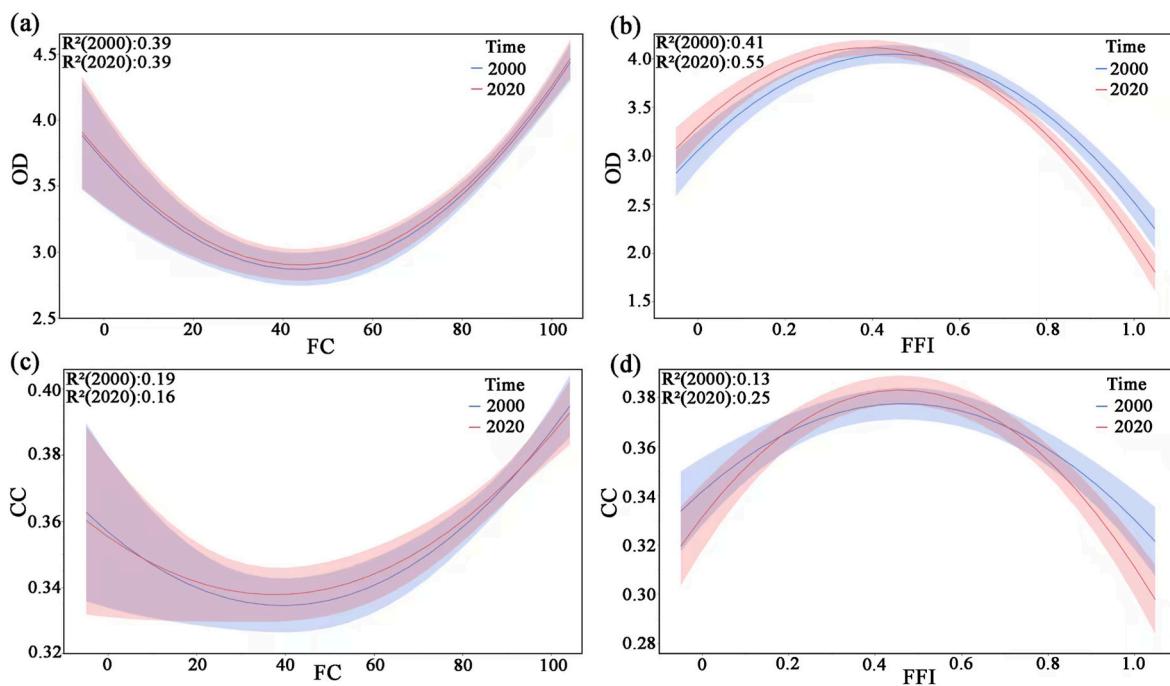


Fig. 4. Associations between diversity (OD) and community completeness (CC) and forest coverage in tropical plantation forests (rotation ≤ 15 years; F32) based on the second-order polynomials. FC represents forest coverage. FFI represents forest fragmentation index. The shaded band is a pointwise 95 % confidence interval on the fitted values. The red lines represented fitted lines of second-order polynomial for temperate planted forests (rotation > 15 years; F31) and blue lines represent fitted lines of second-order polynomial for tropical plantation forests (rotation ≤ 15 years; F32). All the relationships were significant at the $P < 0.1$ level.

(Sloan et al., 2019; Ma et al., 2023). Rotational activities can lead to rapid and transformative changes in tropical plantation forest coverage (Sloan et al., 2016, 2019). At the beginning of forest recovery, this leads to increased light availability on the forest floor, which can favor shade-intolerant species and potentially decrease the diversity of shade-tolerant species (Beaudet et al., 2004; Anderson-Teixeira et al., 2013). Large areas of tropical plantation forests can provide suitable habitats for stabilizing forest communities (Zhu et al., 2004; Lesiv et al., 2022; Wan et al., 2024). The connectivity of habitat patches significantly affected species dispersal rates and patterns (Riibak et al., 2015, 2017). Increasing forest coverage, connectivity, or the ability of species to move between patches can increase colonization rates and potentially reduce extinction rates, particularly in fragmented landscapes (Uroy et al., 2019; Naaf et al., 2021; Ma et al., 2023). More species may enter plant communities of tropical plantation forests during the late rotation period (Chazdon et al., 2007); consequently, the dynamic process whereby there is a balance between species addition (via immigration or speciation) and loss (via emigration or extinction) in tropical plantation forests may be maintained under short rotation time (Olivares et al., 2018; Wu et al., 2020; Cramer and Verboom, 2024). Accordingly, community completeness in tropical plantation forests (rotation ≤ 15 years) should be used as an index to monitor species diversity and ecosystem function based on forest coverage assessments.

For each of the two years assessed in this study, we observed that the increasing forest fragmentation tended to result in the initially increasing and then decreasing observed diversity, dark diversity, and community completeness in tropical plantation forests (rotation ≤ 15 years). Overall, high levels of forest fragmentation may lead to low observed diversity, dark diversity, and community completeness, resulting in negative effects on biodiversity conservation and ecological restoration. High levels of forest fragmentation in tropical plantation forests reflect habitat loss (Naaf et al., 2021); consequently, tropical forests provide limited niche space for species dispersal and migration (Pulliam, 2000; Naaf et al., 2021). Thus, plant communities in tropical

forests tend to be limited by minimum population size, species interactions, and niche characteristics established by the environment (Pulliam, 2000; Wiens, 2011). Fragmentation leads to smaller isolated forest patches with reduced species richness, altered plant community composition, and decreased representation of mature forest species, resulting in low observed diversity and community completeness (Riibak et al., 2015, 2017; Calcagno et al., 2022). In addition to habitat loss, anthropogenic disturbances such as the felling of trees, illegal harvesting of plants, and human-induced wildfires can cause unsuitable habitats and local extinctions in tropical planted forests (rotation ≤ 15 years; Michalski and Peres, 2005; Burkle et al., 2015; Hughes, 2017). Thus, dark diversity may be negatively related to forest fragmentation in tropical plantation forests (rotation ≤ 15 years).

Overall, dark diversity was positively associated with forest fragmentation in temperate planted forests (rotation > 15 years) in 2000 and 2020, thereby indicating that forest fragmentation may contribute to missing species in plant communities due to the small size of the species pools in temperate planted forests. Moreover, regional human impacts can influence natural ecosystems of temperate planted forests through forest cultivation and cutting, which poses a serious threat to plant diversity, creating conditions that are disproportionately favorable to a few competitively superior species at the expense of a large number of other species (Pulliam, 2000; Nguon and Kulakowski, 2013; Zhou et al., 2013; Naaf et al., 2021; Lapola et al., 2023). Monitoring the dynamics of fragmentation in temperate planted forests (rotation > 15 years) is necessary to maintain a high diversity of plant species based on the assessment of dark diversity. Hence, we need to highlight that long-time rotation may lead to high dark diversity, providing important references for ecological restoration. Next, the planting density should be enhanced (Ekholm et al., 2023). Planting forests with diverse species and low forest fragmentation can help ensure their success, promote the transition of dark diversity to observed diversity, and increase community completeness.

For each of the two years assessed in this study, our findings revealed

that the negative effects of forest fragmentation on dark diversity (i.e., lightly increasing and then decreasing) in tropical plantation forests (rotation ≤ 15 years) were opposite to those in temperate planted forests (rotation > 15 years). Although tropical plantation forests favor large species pools, their short rotation time may lead to long edges, high isolation, and large patch sizes, resulting in high levels of forest fragmentation (Roberge et al., 2016; Hansen et al., 2020). Species may become locally extinct due to certain adverse circumstances or stochastic population dynamics and decline in numbers due to unsuitable growth and survival conditions in the region (Lande, 1993). Furthermore, limitations in species dispersal prevent the colonization of suitable sites, both of which may be influenced by anthropogenically associated habitat loss in tropical forests (Riibak et al., 2015, 2017; Pulliam, 2000; Naaf et al., 2021). Thus, the low dark diversity may have occurred because of high forest fragmentation and short rotation time. However, the situation in temperate planted forests (rotation > 15 years) is different. Temperate-planted forests promote a high dispersal ability to drive plant species with the potential to respond to disturbances and invest seeds in persistence, which is characteristic of highly fragmented and isolated habitats (Gilbert and Lechowicz, 2004; McEuen and Curran, 2004). Extensive forest fragmentation may lead to recolonization and establishment of plant species with strong competitive abilities in temperate planted forests under rotation activities (Gilbert and Lechowicz, 2004; Soubeyrand et al., 2023). A long rotation time could provide suitable ecological niches for the available plant species within a limited species pool (McEuen and Curran, 2004). Forest fragmentation had positive effects on dark diversity within temperate plantation forests (rotation > 15 years) and may replace species diversity with fewer species, as the latter can reduce the local diversity of plant life. If the planted trees are non-native to an area, they can become invasive, outcompete native species, and further reduce plant species diversity (Bennett et al., 2016; Wang and Wan, 2021). Hence, the contrasting effects of forest fragmentation on dark diversity between tropical plantation forests (with rotation ≤ 15 years) and temperate planted forests (with rotation > 15 years) exit due to the type of biome and rotation time and have different management implications for the conservation and restoration of plant diversity.

4.1. Limitations and practical implications

Our study provided effective evidence linking forest coverage and fragmentation to the dark diversity of plant communities under different forest management practices; however, it has certain limitations. First, more plots should be used to assess the dark diversity of plant communities under different forest management practices. We used a variety of databases to assess the observed diversity, dark diversity, and community completeness; however, sampling bias still persisted. For example, the high sampling density was distributed in Europe and the Americas, but Africa may not have been analyzed due to a lack of data. Future studies should include more plots to estimate the dark diversity in plant communities. Second, we explored whether forest coverage and fragmentation were linked to the dark diversity of plant communities at spatial and temporal scales. Experimental studies should be conducted to further validate our results. Although rotation experiments have been conducted worldwide, few studies have attempted to assess the dark diversity of plant communities (Ekholm et al., 2023). Hence, future studies should integrate rotation experiments with dark diversity estimations to guide the effective development of forest management practices. Third, the stacked sums of species suitability (i.e., dark diversity) might be inflated by the number of species in each region because, based on the hypergeometric method, all absent species will have a probability of being part of the species pool. The approaches used in our study have been widely applied to the estimation of dark diversity. Future studies should develop more effective approaches to estimate the dark diversity of plant communities at different spatial scales.

Different forest management practices can contribute to biodiversity

conservation and ecosystem management at spatial and temporal scales. Dark diversity, coupled with community completeness, should be used to assess the conservation and restoration status of forests, thereby enhancing the efficacy of forest management practices worldwide. Here, we were only able to establish significant effects of forest coverage and fragmentation on dark diversity and community completeness in tropical plantation forests (rotation ≤ 15 years) and temperate plantation forests (rotation > 15 years). However, these results indicated that the effects of forest coverage and fragmentation on dark diversity should be considered in the context of the distinction between tropical and temperate biomes. Accordingly, we developed models to predict the dynamics of high community completeness in plant communities based on dark diversity using forest coverage and fragmentation as predictors, along with rotation time and biome type. For the associations between forest coverage and fragmentation, dark diversity, and community completeness, we propose that rotational actions should not lead to forest fragmentation and favor high dark diversity and community completeness. Hence, edge density, patch density, and mean patch area (i.e., indices of forest fragmentation) should be applied to guide the rotation patterns of plantation forests to maintain highly complete plant communities.

5. Conclusions

The dark diversity of plant communities is largely determined by forest coverage and fragmentation and can thus be used as a direct indicator of plant diversity for conservation and restoration management. We established that these indicators would be most effective for tropical plantation forests (with rotation ≤ 15 years) and temperate planted forests (with rotation > 15 years). Dark diversity and community completeness should be applied to predict changing trends in the species diversity of plant communities, using forest coverage and fragmentation as immediate indicators and services for biodiversity conservation. Moreover, it is important to understand the dynamics of plant species diversity in relation to the type of biome and rotation time. Further analyses should be conducted to apply the concept of dark diversity to biodiversity conservation and management.

CRediT authorship contribution statement

Ji-Zhong Wan: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Xiaodan Wang:** Writing – review & editing, Supervision, Project administration.

Data availability statement

Data are available on request. The other data including forest coverage, fragmentation and management practice were collected from open-access databases.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This project was financially supported by the Hundred Talent Program of Chinese Academy of Sciences (No. E4K2150150). We thank the editors and the two reviewers for their comments on the improvement of the manuscript. We are grateful to Prof. Dr. Brian Enquist, Dr. Brian Maitner, Prof. Dr. Pablo Marquet and Dr. Chun-Jing Wang for supporting the BIEN database. We thank Prof. Dr. Pablo Marquet for the support

of the workshop organization and data collection under Fondecyt projects (Nos. 3180028 and 3190073). We thank the BIEN contributors for supporting plot databases as follows: Acadia National Park, Agate Fossil Beds National Monument, Carolina Vegetation Survey, New Zealand National Vegetation Survey, Gillespie, U.S. Forest Inventory and Analysis (FIA) National Program, The Madidi Project, Gentry Transect Dataset, Alvar NYHP, Angelina National Forest, Apalachicola National Forest, Badlands National Park, Bankhead National Forest, Barro Colorado Nature Monument-Soberania National Park, Bonifacino Forest Transects, Brad Boyle Forest Transects, Bukit Barisan, Bwindi Impenetrable Forest, Cam Webb Borneo Plots, Caxiuana, Central Suriname Nature Reserve, Chattahoochee National Forest, Cherokee National Forest, Cocha Cashu-Manu National Park, Colorado Wetland and Riparian Classification, Composition and function of vegetation alliances in the Interior Northwest, USA, Congaree Swamp National Monument, Croatan National Forest, CTFS Panama Plots, Davy Crockett National Forest, Delta National Forest, Devils Tower National Monument, DeWalt Bolivia forest plots, Effigy Mounds National Monument, Fire Island National Seashore, Fort Hood Vegetation Map, Fort Laramie National Historic Site, Glacier National Park, Grasslands of Glacier National Park, Great Smoky Mountains National Park, Harpers Ferry National Historic Park, Holly Springs National Forest, Isle Royale National Park, Jewel Cave National Monument, Korup National Park, LaFramboise Island Management Plan, La Selva Secondary Forest Plots, Madidi, Manaus, M. D. Walker Pingo Study, Misc plots from nw SD, Mississippi Vegetation Survey, MN NHP Releve Database, Mount Rushmore National Memorial, Nam Kading, Noel Kempff Forest Plots, Noel Kempff Savanna Plots, Nouabalé Ndoki, NYNHP database dump 2004, Ocala National Forest, Oconee National Forest, Osceola National Forest, Pasoh Forest Reserve, Pawnee Grassland Classification, Pilon Lajas Treeplots Bolivia, RAINFOR-0.1 ha Madre de Dios, Peru, RAINFOR – 1 ha Peru, Ranomafana, Rock Creek Park, Sabine National Forest, Sam Houston National Forest, Scheiner: Species enrichment in a transitional landscape, northern lower Michigan, Shenandoah National Park, Short Mountain Wildlife Management Area, Southwest GAP, Arizona, Southwest GAP, ColoradoSouthwest GAP, Nevada, Southwest GAP, New Mexico, Southwest GAP, Utah, St. Francis National Forest, Talladega-Oakmulgee National Forest, Talladega-Talladega National Forest, Theodore Roosevelt National Park, Tuskegee National Forest, Udzungwa, Valley Forge National Historic Park, Vegetation of the east slope of the Colorado Front Range, Volcán Barva, Voyageurs National Park, Waterton Lakes National Park, Wind Cave National Park, Yanachaga Chimillén National Park, Yosemite National Park, Zion National Park, and Zion National Park 1987–1989 vegetation survey. We thank the sPlotOpen contributors for supporting plot databases as follows: [ForestPlots.net](#), SALVIAS, Vegetation Database of Eurasian Tundra, Tundra Vegetation Plots (TundraPlot), Vegetation Database Forest of Southern Ural, Database of Masaryk University's Vegetation Research in Siberia, Database Meadows and Steppes of Southern Ural, Forest Vegetation Database of Turkey-FVDT, West African Vegetation Database, BIOTA Southern Africa Biodiversity Observatories Vegetation Database, SWEA-Dataveg, PANAF Vegetation Database, Vegetation Database of the Okavango Basin, Sahel Vegetation Database, Forest Database of Central Congo Basin, Vegetation Database of Ethiopia, Vegetation Database of Southern Morocco, Vegetation Database of Zimbabwe, Korean Forest Database, Vegetation of Middle Asia, Rice Field Vegetation Database, Tropical Forest Dataset of Bangladesh, China Forest-Steppe Ecotone Database, Tibet-PaDeMoS Grazing Transect, Vegetation Database of the BEF China Project, Vegetation Database of the Northern Mountains in China, Vegetation Database of Sinai in Egypt, Sulawesi Vegetation Database, Vegetation Database of Iran, Database of Meadow Vegetation in the NW Tien Shan Mountains, Southern Gobi Protected Areas Database, Wetland Vegetation Database of Baikal Siberia (WETBS), Database of Siberian Vegetation (DSV), Database of the University of Münster-Biodiversity and Ecosystem Research Group's Vegetation Research in Western Siberia and Kazakhstan, Vegetation Database of Saudi Arabia, Eastern Pamirs,

National Vegetation Database of Taiwan, Socotra Vegetation Database, AEKOS, New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN), New Zealand National Vegetation Databank, Forest Plots from Papua New Guinea, Nordic-Baltic Grassland Vegetation Database (NBGVD), Vegetation-Plot Database of the University of the Basque Country (BIOVEG), Balkan Dry Grasslands Database, Mediterranean Ammophiletea Database, European Coastal Vegetation Database, The Nordic Vegetation Database, Balkan Vegetation Database, WetVegEurope, European Mire Vegetation Database, Vegetation Database of Albania, Austrian Vegetation Database, INBOVEG, Bulgarian Vegetation Database, Swiss Forest Vegetation Database, Czech National Phytosociological Database, VegMV, VegetWeb Germany, German Vegetation Reference Database (GVRD), National Vegetation Database of Denmark, Iberian and Macaronesian Vegetation Information System (SIVIM)-Wetlands, SOPHY, UK National Vegetation Classification Database, KRITI, Hellenic Natura 2000 Vegetation Database (HelNatVeg), Hellenic Woodland Database, Phytosociological Database of Non-Forest Vegetation in Croatia, Croatian Vegetation Database, CoenoDat Hungarian Phytosociological Database, VegItaly, Vegetation database of Habitats in the Italian Alps-HabitAlp, Vegetation-Plot Database Sapienza University of Rome (VPD-Sapienza), Lithuanian Vegetation Database, Semi-natural Grassland Vegetation Database of Latvia, Vegetation Database of the Republic of Macedonia, Dutch National Vegetation Database, Polish Vegetation Database, Romanian Forest Database, Romanian Grassland Database, Vegetation Database Grassland Vegetation of Serbia, Lower Volga Valley Phytosociological Database, Vegetation Database of the Volga and the Ural Rivers Basins, Vegetation Database of Tatarstan, Vegetation Database of Slovenia, Slovak Vegetation Database, Ukrainian Grasslands Database, Vegetation Database of Ukraine and Adjacent Parts of Russia, Tree Biodiversity Network (BIOTREE-NET), Database of Timberline Vegetation in NW North America, Understory of Sugar Maple Dominated Stands in Quebec and Ontario (Canada), Boreal Forest of Canada, Vegetation, Database of Greenland, VegBank, Carolina Vegetation Survey Database, Alaska-Arctic Vegetation Archive, VegPáramo, Vegetation Database of Central Argentina, Bolivia Forest Plots, Forest Inventory, State of Santa Catarina, Brazil (IFFSC Project), Grasslands of Rio Grande do Sul, Brazil, Grassland Database of Campos Sulinos, SSAForests_Plots_db, Chilean Park Transects-Fondecyt 1040528, and Ecuador Forest Plot Database.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.126408>.

Data availability

Data will be made available on request.

References

- Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., DeLucia, E.H., 2013. Altered dynamics of forest recovery under a changing climate. *Glob. Change Biol.* 19, 2001–2021.
- Arnesi, E.A., López, D.R., Barberis, I.M., 2024. Relationship between degradation and the structural-functional complexity of subtropical xerophytic forests in the Argentine Wet Chaco. *For. Ecol. Manag.* 562, 121957.
- Beaudet, M., Messier, C., Leduc, A., 2004. Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. *J. Ecol.* 92, 328–338.
- Bell, F.W., Lamb, E.G., Sharma, M., Hunt, S., Anand, M., Dacosta, J., Newmaster, S.G., 2016. Relative influence of climate, soils, and disturbance on plant species richness in northern temperate and boreal forests. *For. Ecol. Manag.* 381, 93–105.
- Bennett, J.A., Riibak, K., Kook, E., Reier, Ü., Tamme, R., Guillermo Bueno, C., Pärtel, M., 2016. Species pools, community completeness and invasion: disentangling diversity effects on the establishment of native and alien species. *Ecol. Lett.* 19, 1496–1505.
- Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P., Meurisse, N., Oxbridge, A., Taki, H., Ian, D., Thompson, I. D., Plas, F., Jactel, H., 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers. Conserv.* 26, 3005–3035.

- Brown, M.J., Walker, B.E., Black, N., Govaerts, R.H., Ondo, I., Turner, R., Nic Lughadha, E., 2023. rWCP: a companion R package for the world checklist of vascular plants. *New Phytol.* 240, 1355–1365.
- Burkle, L.A., Myers, J.A., Belote, R.T., 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. *Ecosphere* 6, 1–14.
- Calcagno, V., Cunniffe, N.J., Hamelin, F.M., 2022. Metacommunity dynamics and the detection of species associations in co-occurrence analyses: why patch disturbance matters. *Funct. Ecol.* 36, 1483–1499.
- Carmona, C.P., Pärtel, M., 2021. Estimating probabilistic site-specific species pools and dark diversity from co-occurrence data. *Global Ecol. Biogeogr.* 30, 316–326.
- Carstensen, D.W., Lessard, J.P., Holt, B.G., Krabbe Borregaard, M., Rahbek, C., 2013. Introducing the biogeographic species pool. *Ecography* 36, 1310–1318.
- Chazdon, R.L., Letcher, S.G., Van Breugel, M., Martínez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary neotropical forests following major disturbances. *Philos. Trans. R. Soc. B* 362, 273–289.
- Chollet, S., Dano, M., Thiébaut, G., Jung, V., 2025. Dark diversity and habitat conservation status: two sides of the same coin for conservation and restoration? *Ecol. Indic.* 170, 112990.
- Cousins, S.A., Ohlson, H., Eriksson, O., 2007. Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landscape Ecol.* 22, 723–730.
- Cramer, M.D., Verboom, G.A., 2024. Evidence that species richness begets species richness. *J. Biogeogr.* 51, 659–674.
- De Bello, F., Fibich, P., Zelený, D., Kopecký, M., Mudrák, O., Chytrý, M., Pyšek, P., Wild, J., Michálová, D., Sádlo, J., Smilauer, P., Lepš, J., Pärtel, M., 2016. Measuring size and composition of species pools: a comparison of dark diversity estimates. *Ecol. Evol.* 6, 4088–4101.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., De Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Kloser, H., Shennan-Farpon, Y., Kindt, R., Lillesø, J.P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67, 534–545.
- Ekholm, A., Lundqvist, L., Axelsson, E.P., Egnell, G., Hjälterén, J., Lundmark, T., Sjögren, J., 2023. Long-term yield and biodiversity in stands managed with the selection system and the rotation forestry system: a qualitative review. *For. Ecol. Manag.* 537, 120920.
- Führer, E., 2000. Forest functions, ecosystem stability and management. *For. Ecol. Manag.* 132, 29–38.
- Gilbert, B., Lechowicz, M.J., 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Natl. Acad. Sci. USA* 101, 7651–7656.
- Hansen, M.C., Wang, L., Song, X.P., Tyukavina, A., Turubanova, S., Potapov, P.V., Stehman, S.V., 2020. The fate of tropical forest fragments. *Sci. Adv.* 6, eaax8574.
- Hughes, A.C., 2017. Understanding the drivers of S outeast A sian biodiversity loss. *Ecosphere* 8, e01624.
- Jakovac, C.C., Junqueira, A.B., Crouzeilles, R., Peña-Claros, M., Mesquita, R.C., Bongers, F., 2021. The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biol. Rev.* 96, 1114–1134.
- Jeliazkov, A., Mijatović, D., Chantepie, S., Andrew, N., Arlettaz, R., Barbaro, L., Barsoum, N., Bartonova, A., Belskaya, E., Bonada, N., Brind'Amour, A., Carvalho, R., Castro, H., Chmura, D., Choler, P., Chong-Seng, K., Cleary, D., Cormont, A., Cornwell, W., de Campos, R., de Voogd, N., Doledec, S., Drew, J., Dziock, F., Eallondo, A., Edgar, M.J., Farmeda, F., Hernandez, D.F., Frenette-Dussault, C., Fried, G., Gallardo, B., Gibb, H., Gonçalves-Souza, T., Higuti, J., Humbert, J.Y., Krasnov, B.R., Saux, E.L., Lindo, Z., Lopez-Baucells, A., Lowe, E., Marteindottir, B., Martens, K., Meffert, P., Mellado-Díaz, A., Menz, M.H.M., Meyer, C.F.J., Miranda, J. R., Mouillet, D., Ossola, A., Pakeman, R., Pavoinne, S., Pekin, B., Pino, J., Pocheville, A., Pomati, F., Poschlod, P., Prentice, H.C., Puschke, O., Raever, V., Reitalu, T., Renema, W., Ribera, I., Robinson, N., Robroek, B., Rocha, R., Shieh, S.H., Spake, R., Staniak-Kik, M., Stanko, M., Tejerina-Garro, F.L., ter Braak, C., Urban, M.C., van Klink, R., Villéger, S., Wegman, R., Westgate, M.J., Wolff, J., Żarnowiec, J., Zolotarev, M., Chase, J.M., 2020. A global database for metacommunity ecology, integrating species, traits, environment and space. *Sci. Data* 7, 6.
- Jin, Y.L., Wang, H.Y., Wei, L.F., Hou, Y., Hu, J., Wu, K., Xia, H.J., Xia, J., Zhou, B.R., Li, K., Ni, J., 2022. A plot-based dataset of plant community on the Qingzang Plateau. *Chinese J. Plant Ecol.* 46, 846–854.
- Lai, J., Zou, Y., Zhang, S., Zhang, X., Mao, L., 2022. glmmhp: an R package for computing individual effect of predictors in generalized linear mixed models. *J. Plant Ecol.* 15, 1302–1307.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142, 911–927.
- Lapola, D.M., Pinho, P., Barlow, J., Aragão, L.E., Berenguer, E., Carmenta, R., Liddy, H. M., Seixas, H., Silva, C.V.J., Silva-Junior, C.H.I., Alencar, A.A.C., Anderson, L.O., Armenteras, D., Brovkin, V., Calders, K., Chambers, J., Chini, L., Costa, M.H., Faria, B.L., Fearnside, P.M., Ferreira, J., Gatti, L., Gutierrez-Velez, V.H., Han, Z., Hibbard, K., Koven, C., Lawrence, P., Pongratz, J., Portela, B.T.T., Rounsevell, M., Ruane, A.C., Schaldach, R., da Silva, S.S., von Randow, C., Walker, W.S., 2023. The drivers and impacts of Amazon forest degradation. *Science* 379, eabp8622.
- Lesiv, M., Schepaschenko, D., Buchhorn, M., See, L., Dürrauer, M., Georgieva, I., Jung, M., Hofhansl, F., Schulze, K., Bilous, A., Blyshchyk, V., Mukhortova, L., Brenes, C.L.M., Krivobokov, L., Ntie, S., Tsogt, K., Pietsch, S.A., Tikhonova, E., Kim, M., Fritz, S., 2022. Global forest management data for 2015 at a 100 m resolution. *Sci. Data* 9, 199.
- Lewis, R.J., de Bello, F., Bennett, J.A., Fibich, P., Finerty, G.E., Götzemberger, L., Hiiresalu, I., Kasari, L., Lepš, J., Májeková, M., Mudrák, O., Riibak, K., Ronk, A., Rychtecká, T., Vitová, A., Pärtel, M., 2017. Applying the dark diversity concept to nature conservation. *Conserv. Biol.* 31, 40–47.
- Liebsch, D., Velasco, S.J.E., Mikich, S.B., Marques, M.C., Galvao, F., 2021. Effects of selective logging, fragmentation, and dominance of bamboos on the structure and diversity of Araucaria Forest fragments. *For. Ecol. Manag.* 487, 118961.
- Ma, J., Li, J., Wu, W., Liu, J., 2023. Global forest fragmentation change from 2000 to 2020. *Nat. Commun.* 14, 3752.
- Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff, C.E., Jørgensen, P.M., Kraft, N.J., McGill, B., 2018. The bien r package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol. Evol.* 9, 373–379.
- McEuen, A.B., Curran, L.M., 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. *Ecology* 85, 507–518.
- Michalski, F., Peres, C.A., 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biol. Conserv.* 124, 383–396.
- Mitchell, M.G., Bennett, E.M., Gonzalez, A., 2014. Forest fragments modulate the provision of multiple ecosystem services. *J. Appl. Ecol.* 51, 909–918.
- Moëslund, J.E., Brunbjerg, A.K., Clausen, K.K., Dalby, L., Fløjgaard, C., Juel, A., Lenoir, J., 2017. Using dark diversity and plant characteristics to guide conservation and restoration. *J. Appl. Ecol.* 54, 1730–1741.
- Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *J. Appl. Ecol.* 54, 12–27.
- Naaf, T., Feigs, J.T., Huang, S., Brunet, J., Cousins, S.A., Decocq, G., Frenne, P.D., Diekmann, M., Govaert, S., Hedwall, P.O., Helsen, K., Lenoir, J., Liira, J., Meeussen, C., Plue, J., Poli, P., Spicher, F., Vangansbeke, P., Vanneste, T., Verheyen, K., Stephanie, I.J., Holzhauer, S.I.J., Kramp, K., 2021. Sensitivity to habitat fragmentation across European landscapes in three temperate forest herbs. *Landscape Ecol.* 36, 2831–2848.
- Nguon, P., Kulakowski, D., 2013. Natural forest disturbances and the design of REDD+ initiatives. *Environ. Sci. Pol.* 33, 332–345.
- Noreika, N., Pärtel, M., Öckinger, E., 2020. Community completeness as a measure of restoration success: multiple-study comparisons across ecosystems and ecological groups. *Biodivers. Conserv.* 29, 3807–3827.
- Olivares, I., Karger, D.N., Kessler, M., 2018. Assessing species saturation: conceptual and methodological challenges. *Biol. Rev.* 93, 1874–1890.
- Pagel, J., Schurr, F.M., 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecol. Biogeogr.* 21, 293–304.
- Pärtel, M., Szava-Kovats, R., Zobel, M., 2011. Dark diversity: shedding light on absent species. *Trends Ecol. Evol.* 26, 124–128.
- Pärtel, M., Szava-Kovats, R., Zobel, M., 2013. Community completeness: linking local and dark diversity within the species pool concept. *Folia Geobot.* 48, 307–317.
- Pärtel, M., Tamme, R., Carmona, C.P., Riibak, K., Moora, M., Bennett, J.A., Chiarucci, A., Chytrý, M., Bello, F.D., Eriksson, O., Harrison, S., Lewis, R.J., Moles, A.T., Öpik, M., Price, J.N., Amputu, V., Askarizadeh, D., Atashgahi, Z., Aubin, I., Azcarate, F.M., Barrett, M.D., Bashirzadeh, M., Bátori, Z., Beenaerts, N., Bergholz, K., Birkeli, K., Biurrun, I., Blanco-Moreno, J.M., Bloodworth, K.J., Boisvert-Marsh, L., Boldgiv, B., Brancalion, P.H.S., Brearley, F.Q., Brown, C., Bueno, C.G., Buffa, G., Cahill, J.F., Campos, J.A., Cangelmi, G., Carbognani, M., Carcailliet, C., Cerabolini, B.E.L., Chevalier, R., Clavel, J.S., Costa, J.M., Cousins, S.A.O., Čuda, J., Dairel, M., Fratte, M.D., Danilova, A., Davison, J., Deák, B., Vecchio, S.D., Dembicz, I., Dengler, J., Dolezal, J., Domene, X., Dvorský, M., Ejtehadi, H., Enrico, L., Epikhin, D., Eskelinen, A., Essl, F., Fan, G., Fantinato, E., Fazlioglu, F., Fernández-Pascual, E., Ferrara, A., Fidelis, A., Fischer, M., Flagmeier, M., Forte, T.G.W., Fraser, L.H., Fujinuma, J., Furquim, F.F., Garris, B., Garris, H.W., Giorgis, M.A., Galdo, G.G.D., González-Robles, A., Good, M.K., Guardiola, M., Guarino, R., Guerrero, I., Guillermo, J., Güller, B., Guo, Y.J., Haesen, S., Hejda, M., Heleno, R.H., Høye, T.T., Hrvícnák, R., Huang, Y.X., Hunter, J.T., Iakushenko, D., Ibáñez, R., Ingerpuu, N., Irl, S.D.H., Janíková, E., Jansen, F., Jeitsch, F., Jentsch, A., Jiménez-Alfaro, B., Jók, M., Jouri, M.H., Karami, S., Katal, N., Kelemen, A., Khairullin, B., Khuuro, A.A., Komatsu, K.J., Konečná, M., Kook, E., Korell, L., Koroleva, N., Korznikov, K.A., Kozhevnikova, M.V., Kozub, L., Laanisto, L., Lager, H., Lanta, V., Lasagno, R.G., Lembrechts, J.J., Li, L.P., Lisner, A., Liu, H., Liu, K., Liu, X.H., Lucas-Borja, M.E., Ludewig, K., Lukács, K., Luther-Mosebach, J., Macek, P., Marignani, M., Michalet, R., Miglécz, T., Moeslund, J.E., Moeyis, K.M., Montesinos, D., Moreno-Jiménez, E., Moysienco, I., Mucina, L., Muñoz-Rojas, M., Murillo, R.A., Nambahu, S.M., Neuenkamp, L., Normand, S., Nowak, A., Nuche, P., Oja, T., Onipchenko, V.G., Pachedjeva, K.L., Paganelli, B., Peco, B., Peralta, A.M.L., Pérez-Haase, A., Peri, P.L., Petraglia, A., Peyre, G., Plaza-Álvarez, P.A., Plue, J., Prentice, H.C., Prokhorov, V.E., Radujković, D., Rahamanian, S., Reitalu, T., Ristow, M., Robin, A.A., Robles, A.B., Ginart, D.A.R., Román, R., Roos, R.E., Rosati, L., Sádlo, J., Salimbayeva, K., Dios, R.S.D., Sanchir, K., Sattler, C., Scasta, J., D., Schmiedel, U., Schrader, J., Schultz, N.L., Sellan, G., Serra-Díaz, J.M., Silan, G., Skálová, H., Skobel, N., Sonkoly, J., Stajerová, K., Svitková, I., Swierszcz, S., Tanentzap, A.J., Tanentzap, F.M., Tarifa, R., Tejero, P., Tekkeev, D.K., Tholin, M., Thormodsæter, R.S., Tian, Y.C., Tokaryuk, A., Tölgysi, C., Tomaselli, M., Tordoni, E., Török, P., Tóthmérész, B., Toussaint, A., Touzard, B., Trindade, D.P.E., Tsakalos, J.L., Türkis, S., Valencia, E., Valerio, M., Valkó, O., Van Meerbeek, K., Vandvik, V., Villegas, J., Virtanen, R., Vítová, M., Vojík, M., Hessberg, A.V., Oppen, J.V., Wagner, V., Wan, J.Z., Wang, C.J., Wani, S.A., Weiss, L., Wevill, T.,

- Xiao, S., Martínez, O.Z., Martin Zobel, M., 2025. Global impoverishment of natural vegetation revealed by dark diversity. *Nature* 641, 917–924.
- Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3, 349–361.
- Ramírez-Delgado, J.P., Di Marco, M., Watson, J.E., Johnson, C.J., Rondinini, C., Corredor Llano, X., Arias, M., Venter, O., 2022. Matrix condition mediates the effects of habitat fragmentation on species extinction risk. *Nat. Commun.* 13, 595.
- Riibak, K., Bennett, J.A., Kook, E., Reier, Ü., Tamme, R., Bueno, C.G., Pärtel, M., 2020. Drivers of plant community completeness differ at regional and landscape scales. *Agric. Ecosyst. Environ.* 301, 107004.
- Riibak, K., Noreika, N., Helm, A., Öpik, M., Kook, E., Kasari-Toussaint, L., Jöks, M., Paganelli, B., Martínez, O.Z., Tullus, H., Tullus, Y., Lutter, R., Oja, E., Saag, A., Randlane, T., Pärtel, M., 2024. Plants, fungi, and carabid beetles in temperate forests: both observed and dark diversity depend on habitat availability in space and time. *Lands. Ecol.* 39, 158.
- Riibak, K., Reitalu, T., Tamme, R., Helm, A., Gerhold, P., Znamenskiy, S., Bengtsson, K., Rosén, E., Prentice, H.C., Pärtel, M., 2015. Dark diversity in dry calcareous grasslands is determined by dispersal ability and stress-tolerance. *Ecography* 38, 713–721.
- Riibak, K., Ronk, A., Kattge, J., Pärtel, M., 2017. Dispersal limitation determines large-scale dark diversity in Central and Northern Europe. *J. Biogeogr.* 44, 1770–1780.
- Roberge, J.M., Laudon, H., Björkman, C., Ranius, T., Sandström, C., Felton, A., Sténs, A., Nordin, A., Granström, A., Widemo, F., Bergh, J., Sonesson, J., Stenlid, J., Lundmark, T., 2016. Socio-ecological implications of modifying rotation lengths in forestry. *Ambio* 45, 109–123.
- Ronk, A., Szava-Kovats, R., Pärtel, M., 2015. Applying the dark diversity concept to plants at the European scale. *Ecography* 38, 1015–1025.
- Sabatini, F.M., Lenoir, J., Hattab, T., Arnst, E.A., Chytrý, M., Dengler, J., De Ruffray, P., Hennekens, S.M., Jandt, U., Jansen, F., Jimenez-Alfaro, B., Kattge, J., Levesley, A., Pillar, V.D., Purschke, O., Sandel, B., Sultan, F., Aavik, T., Acic, S., Acosta, A.T.R., Agrillo, E., Alvarez, M., Apostolova, I., Khan, M.A.S.A., Arroyo, L., Attorre, F., Aubin, I., Banerjee, A., Bauters, M., Bergeron, Y., Bergmeier, E., Biurrun, I., Bjorkman, A.D., Bonari, G., Bondareva, V., Brunet, J., Carni, A., Casella, L., Cayuela, L., Cerny, T., Chepinoga, V., Csiky, J., Custerevska, R., De Bie, E., de Gasper, A.L., De Sanctis, M., Dimopoulos, P., Dolezal, J., Dziuba, T., El-Sheikh, M.A.M., Enquist, B., Ewald, J., Fazayeli, F., Field, R., Finckh, M., Gachet, S., Galan-de-Mera, A., Garbolino, E., Gholizadeh, H., Giorgis, M., Golub, V., Alsol, I.G., Grytnes, J.A., Guerin, G.R., Gutierrez, A.G., Haider, S., Hatim, M.Z., Herault, B., Mendoza, G.H., Holzel, N., Homeier, J., Hubau, W., Indreica, A., Janssen, J.A.M., Jedrzejek, B., Jentsch, A., Jurgens, N., Kacki, Z., Kapfer, J., Karger, D.N., Kavagci, A., Kearsley, E., Kessler, M., Khamina, L., Killeen, T., Korolyuk, A., Kreft, H., Kuhl, H.S., Kuzemko, A., Landucci, F., Lengyel, A., Lens, F., Lingner, D.V., Liu, H.Y., Lysenko, T., Mahecha, M.D., Marcenó, C., Martynenko, V., Moeslund, J.E., Mendoza, A.M., Mucina, L., Muller, J.V., Munzinger, J.M., Naqinezhad, A., Noroozi, J., Nowak, A., Onyshchenko, V., Overbeck, G.E., Partel, M., Pauchard, A., Peet, R.K., Penuelas, J., Perez-Haase, A., Peterka, T., Petrik, P., Peyre, G., Phillips, O.L., Prokhorov, V., Rasomavicius, V., Revermann, R., Rivas-Torres, G., Rodwell, J.S., Rusina, S., Samimi, C., Schmidt, M., Schrodt, F., Shan, H.H., Shirokikh, P., Sibik, J., Silc, U., Sklenar, P., Skvorc, Z., Sparrow, B., Sperandii, M.G., Stancic, Z., Svensson, J.C., Tang, Z.Y., Tang, C.Q., Tsiripidis, I., Vanselow, K.A., Martinez, R.V., Vassilev, K., Velez-Martin, E., Venanzoni, R., Vibrans, A.C., Violette, C., Virtanen, R., von Wehrden, H., Wagner, V., Walker, D.A., Waller, D.M., Wang, H.F., Wesche, K., Whitfeld, T.J.S., Willner, W., Wiser, S.K., Wohlgemuth, T., Yamalov, S., Zobel, M., Bruelheide, H., 2021. sPlotOpen—An environmentally balanced, open-access, global dataset of vegetation plots. *Global Ecol. Biogeogr.* 30, 1740–1764.
- Schlüter, D., Pennell, M.W., 2017. Speciation gradients and the distribution of biodiversity. *Nature* 546, 48–55.
- Serra-Diaz, J.M., Enquist, B.J., Maitner, B., Merow, C., Svensson, J.C., 2017. Big data of tree species distributions: how big and how good? *For. Ecosyst.* 4, 1–12.
- Sloan, S., Goosem, M., Laurance, S.G., 2016. Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. *Lands. Ecol.* 31, 601–618.
- Sloan, S., Meyfroidt, P., Rudel, T.K., Borgers, F., Chazdon, R., 2019. The forest transformation: planted tree cover and regional dynamics of tree gains and losses. *Glob. Environ. Change* 59, 101988.
- Smith, J.R., Letten, A.D., Ke, P.J., Anderson, C.B., Hendershot, J.N., Dhami, M.K., Drott, G.A., Grainger, T.N., Howard, M.E., Morrison, B.M.L., Routh, D., San Juan, P.A., Mooney, H.A., Mordecai, E.A., Crowther, T.W., Daily, G.C., 2018. A global test of ecoregions. *Nature Ecol. Evol.* 2, 1889–1896.
- Soubeyrand, M., Gennaretti, F., Blarquez, O., Bergeron, Y., Taylor, A.R., D'Orangeville, L., Marchand, P., 2023. Competitive interactions under current climate allow temperate tree species to grow and survive in boreal mixedwood forest. *Ecography* 2023, e06525.
- Storch, D., Okie, J.G., 2019. The carrying capacity for species richness. *Global Ecol. Biogeogr.* 28, 1519–1532.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA* 102, 8245–8250.
- Trindade, D.P., Carmona, C.P., Pärtel, M., 2020. Temporal lags in observed and dark diversity in the Anthropocene. *Glob. Change Biol.* 26, 3193–3201.
- Uroy, L., Ernoult, A., Mony, C., 2019. Effect of landscape connectivity on plant communities: a review of response patterns. *Lands. Ecol.* 34, 203–225.
- Wan, J.Z., Pelissier, L., Wang, C.J., Yu, F.H., Li, M.H., 2024. Plant functional composition as an effective surrogate for biodiversity conservation. *Basic Appl. Ecol.* 74, 49–56.
- Wan, J.Z., Wang, C.J., 2023. Legacy effects of historical woodland changes on contemporary plant functional composition. *For. Ecosyst.* 10, 100142.
- Wang, Q., Shang, C., Wang, C.J., Wan, J.Z., 2023. A dataset of quadrat sampling of 455 herb quadrats in Huangshui River Basin, Qinghai Province. *Sci. Data* 8, 328–336.
- Wang, C.J., Huang, S.F., Wu, C.P., Wang, G.N., Wang, L., Zhang, Y.K., Wan, J.Z., 2024. Linear relationships between aboveground biomass and plant species diversity during the initial stage of degraded grassland restoration projects. *Ecol. Evol.* 14, e70128.
- Wang, C.J., Wan, J.Z., 2021. Functional trait perspective on suitable habitat distribution of invasive plant species at a global scale. *Perspect. Ecol. Conserv.* 19, 475–486.
- Wiens, J.J., 2011. The niche, biogeography and species interactions. *Philos. Trans. R. Soc. B* 366, 2336–2350.
- Wu, Y., Chen, Y., Chang, S.C., Chen, Y.F., Shen, T.J., 2020. Extinction debt in local habitats: quantifying the roles of random drift, immigration and emigration. *R. Soc. Open Sci.* 7, 191039.
- Zhang, H., Chase, J.M., Liao, J., 2024. Habitat amount modulates biodiversity responses to fragmentation. *Nat. Ecol. Evol.* 8, 1437–1447.
- Zhou, D., Zhao, S.Q., Liu, S., Oeding, J., 2013. A meta-analysis on the impacts of partial cutting on forest structure and carbon storage. *Biogeosciences* 10, 3691–3703.
- Zhu, H., Xu, Z.F., Wang, H., Li, B.G., 2004. Tropical rain forest fragmentation and its ecological and species diversity changes in southern Yunnan. *Biodivers. Conserv.* 13, 1355–1372.