Perspective Article

The diversity of within-community plant species combinations: A new tool for assessing changes in forests and guiding protection actions

Stefano Chelli [a,1,*], James Lee Tsakalos [a,b,1], Zhengxue Zhu [a], Luciano Ludovico Maria De Benedictis [a], Sandor Bartha [c], Roberto Canullo [a], Liubov Borsukevych [d], Marco Cervellini [a], Giandiego Campetella [a]

[a] School of Biosciences and Veterinary Medicine, University of Camerino, Italy
[b] Harry Butler Institute, Murdoch University, Murdoch, Perth, WA, Australia
[c] Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary
[d] Botanical Garden of Ivan Franko National University of Lviv, Lviv, Ukraine

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ABSTRACT

Biodiversity is changing rapidly, and ecologists use various measures to monitor and conserve it, but not all are equally effective. In the European temperate forests, ecologists are tasked with assessing the impact of global changes on plant species richness; however, this fails at capturing vital information about plant interactions. Using a chronosequence of beech forest stands, spanning 600 years of growth, we demonstrate the application of a different measure of diversity compared to classical species richness in the understorey. This measure, called compositional diversity (CD), considers the number of species combinations and their relative frequency within a community. The response of both classical species richness and CD along with succession, corresponded with our expectations based on ecological theory's U-shape prediction of diversity along the successional gradient. However, after 300 years, there was a significant decoupling between the two measures' responses. While species richness remained low and constant across old-growth and primeval forests, CD peaked in primeval forests, implying that the same number of late-successional species generated more diverse assemblages. This new information emphasises the need to protect old-growth and primeval forests not only to conserve species richness but also to preserve their unique network of species co-occurrence patterns – a factor not well represented by the classical species richness measure.

1. The use of classical diversity measures in forests

Nowhere on earth can such consistently high levels of biodiversity be found than under the canopy of a forest (Sabatini et al., 2022). Ecological theory corroborates the concept that such high levels of diversity are supported by the high number of ecological niches and biotic interactions (Messier et al., 2015), allowing species to coexist in space and time. Under the dappled light stratified by the forest canopy, the irregular distribution of decomposing fallen trees, and natural processes, a mosaic of heterogeneity emerges. This mosaic constitutes the axes along which species percolate within this hypervolume, generating a complex adaptive system (Levin, 1998). Unfortunately, the arrival of humans on the geological clock determined impressive direct (e.g., logging, pollution, fire) and indirect (climate) changes in forest

ecosystems and their diversity (Ammer et al., 2018).

In temperate forests, a mere 1 % of the total biomass represents almost 80 % of the understorey plant richness; this vegetation is essential for maintaining a properly functioning forest ecosystem (Landuyt et al., 2019). Despite the increasing number of diversity indices (e.g., Pavoine, 2020), studies focusing on forest understorey generally attribute changes in the number of species or their relative abundance (i.e., species richness or Shannon diversity) to management practices (e.g., Govaert et al., 2020), the input of pollutants such as nitrogen and sulphur (e.g., Dirnböck et al., 2014), and changes in climatic conditions (e.g., Govaert et al., 2021). These diversity measures are prevalent as biological indicators of sustainable forest management (e. g., SFM; Forest Europe, 2020) applied for conservation and restoration purposes (Paillet et al., 2010; Crouzeilles et al., 2016) and are deeply

entrenched in policy (e.g., European Commission, 2020).

The use of species richness and Shannon diversity as measures for assessing ecological diversity may not always be the most appropriate choice as underscored by Hillebrand et al. (2018). This concern arises due to the assumption of consistent directional trends in species richness resulting from the application of different management strategies (Burrascano et al., 2018), progressive thermophilisation (De Frenne et al., 2013), and increased eutrophication (Verheyen et al., 2012) in European temperate forests. In a comprehensive *meta*-analysis, it was found that there is no significant overall change in species richness, however, the majority of individual studies contained therein demonstrated complete turnover of species over time (Hillebrand et al., 2018). This underscores the need to explore novel methodologies for quantifying shifting diversity in the Anthropocene epoch.

2. The importance of plant interactions

Ecologists study network connections among organisms, including in forest ecosystems (Filotas et al., 2014). These interactions, within and between species, profoundly influence diversity (Callaway & Walker, 1997). For example, epiphytic plants benefit from growing on evergreen trees for moderated light, while plant–soil feedbacks affect soil suitability for other species (e.g., Stanek et al., 2020). Gilbert & Lechowicz (2004) suggest that neutral processes, like random ecological drift, have minimum impact on diversity patterns in temperate forests. Larger interaction networks enhance ecosystem complexity, providing services like pollination and invasion resistance (Lurgi et al., 2014; IPBES, 2019). Unfortunately, classical alpha and beta diversity measures based solely on plot-level species occurrence and abundance fail to capture the intricate biological information arising from complex biotic interactions.

Consider three hypothetical understorey communities with identical number, identity and relative abundance of species (i.e., alpha and beta diversity; Fig. 1). The first community has a random distribution of individuals and species (Fig. 1a), while the other two display patchy distributions. In the first patchy community (Fig. 1b), positive associations (e.g., facilitation) or micro-environmental heterogeneity, enable species coexistence. In the second patchy community (Fig. 1c) negative associations (e.g., competition) or fine-scale environmental heterogeneity, prevent species coexistence. Alpha and beta diversity remain constant across all three hypothetical scenarios, demonstrating that these measures do not adequately convey the biological information arising from the complex network of biotic interactions.

To further illustrate this concept, consider music. The precise arrangement of co-occurring notes can produce a specific composition, such as Beethoven's Fifth Symphony, while randomisation of the same notes will result in a different composition, or even noise. Despite having the same number and frequency of notes (i.e., the same species richness and Shannon diversity), the functions generated by the two musical compositions differ. In parallel, neglecting the variability in species combinations within communities results in the loss of crucial ecological information related to community functions (Juhász-Nagy and Podani, 1983; Bartha et al., 1998).

In this context, we introduce the Compositional Diversity (CD) index, based on species co-occurrence patterns at fine scale (i.e., within community; Juhász-Nagy and Podani, 1983; Tsakalos et al., 2022).
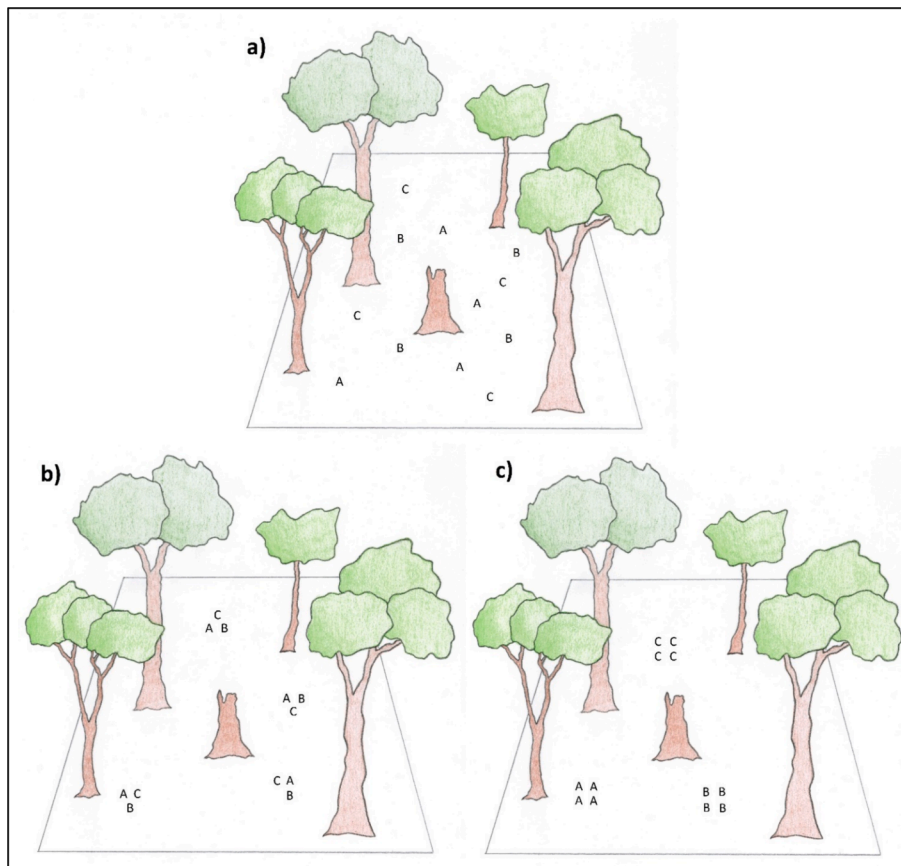

Fig. 1. Three example forest understorey communities with the same species composition (three species represented by different letters in each community) and abundance distribution (four individuals per species) but contrasting spatial patterns. Community (a) is characterised by a random distribution of individuals and species; community (b) is distinguished by aggregation of individuals of different species (positive species associations); community (c) is characterised by aggregation of individuals of the same species (negative species associations).

3. Compositional diversity as a measure of forest complexity in terms of species combinations

Where classical alpha diversity fails to capture the complexity of forest understorey, using beta diversity to describe compositional variation can be advantageous (Anderson et al., 2011). Beta diversity *sensu* Whittaker (1960) is the extent of change in composition between communities, or degree of community differentiation, along with an environmental gradient or a pattern of gradients. Subsequently, studies aiming to equate beta diversity changes with any number of covariates tend to do so at a coarse scale (i.e., macroecological studies; Kraft et al., 2011; Konrád et al., 2023) using plots generally larger than the scale at which biological interactions occur. Assessing patterns of species co-occurrences within a community can benefit from the concept of beta diversity; however, it requires different data sets and methods that can be used to calculate the exact diversity number for a specific spatial scale.

Here, we propose to use one beta diversity measure from Juhász-Nagy's (1967, 1984a, b) information theory models to evaluate within-community patterns of species combinations. Specifically, we used the recent Tsakalos et al.'s (2022) 'comspat' function from the comspat R package to calculate one of Juhász-Nagy's models, namely the Compositional Diversity (CD), as the frequency distribution of realised species combinations within a community expressed as the uncertainty to find a species combination in a sample:

$$H_j(A, B, \cdots, Y) = -\sum\nolimits_{k=1}^{2^s} p_{kj} \, \log \, (p_{kj})$$

Where A, B, …, Y are the *s* species of the community; p_{kj} is the probability of finding a particular species combination (i.e., the kth combination of species) within the sample at a specific sampling unit size *j*; *k* ranges from 1 to 2^s. By varying *j*, CD can be calculated as a function of the spatial scale, with low CD values at very small or large sampling unit sizes, and at least one maximum CD value between these two extremes (Bartha et al., 1998). Due to different assembly constraints, the observed number of species combinations (number of realised species combinations) in natural communities is usually smaller than the theoretical maxima (Bartha, 1992). Higher CD values reflect higher uncertainty in finding a given species combination in a sample, which mirrors a higher variability of species combinations. The method measures the coexistence relationships between species within communities (Podani et al., 1993; Bartha et al., 1998; Tsakalos et al., 2022). It usually relies on recording species at fine scale, within transects or grids composed of several (i.e., hundreds) adjacent sampling units whose size depends on the scale at which biological interactions occur (e.g., resolution of 10 cm x 10 cm or 20 cm x 20 cm for forest understorey layer). In order to provide a practical indication for the application of this method, we estimated that the average sampling time by two trained botanists of a 100 m transect with 1000 sampling units in forest is 90 min. The advantages of using transects are related to (a) reduced sampling time compared to other multiscale or nested sampling designs, (b) minimized disturbance to vegetation during sampling, and (c) maximizing the sample extent with a given sampling effort (see Bartha et al., 2004). Furthermore, with the observation of species presence/absence in 10 cm x 10 cm micro-quadrats, taxonomic errors are rare.

4. Example with a beech forest succession

To evaluate how CD compares to the classical alpha diversity (i.e., species richness), we utilised the U-shaped biodiversity model proposed for forest succession (see Ujházy et al., 2017; Hilmers et al., 2018; Bartha et al., 2020). The model is predicated on the general observation of higher biodiversity in the early and late stages of forest succession (Ujházy et al., 2017; Hilmers et al., 2018; Bartha et al., 2020). Not only this is theoretically interesting, but it is of profound importance to practitioners of forest management and informing on conservation

policy (Hilmers et al., 2018). By studying the variation in biodiversity throughout the entire succession process, we can better understand how different management strategies affect biodiversity and decouple the effect of inherent changes in species as forest develops from climate change (Hilmers et al., 2018).

In our example, we used a successional chronosequence of 30 beech (*Fagus sylvatica* L.) forest stands featuring approximately 5 to about 600 years of development (Fig. 2). The chronosequence consisted of recently logged (0–30 years, n = 8), establishing (30–70, n = 4), early optimum (70–100, n = 3), mid–late optimum (100–200, n = 3), planter–old-growth (200–300, n = 4), old-growth (>300, n = 6) and primeval (never logged, n = 2) stands (structural/age categories modified from Hilmers et al., 2018). In each stand, we established a 100 m circular transect composed of 1,000 contiguous sample units (sized 10 cm x 10 cm or 20 cm x 20 cm) where we recorded the presence of understorey (<1.3 m, i. e., breast height) vascular plant species, including woody and herbaceous species. With data derived from the transect, we measured the total species richness and the maximum CD value. Indeed, the use of maximum CD is suggested to simplify the presentation of community patterns and dynamics (Bartha et al., 1998). Along the successional gradient, we used simple quadratic regressions to test for the U-shaped pattern (Bartha et al., 2020) and visual inspection of the standard error distributions to detect differences between the diversity measures. Our stands selection is interesting because 63 % occur within UNESCO's world heritage listed ancient and primeval beech forests of the Carpathians and other regions of Europe. In detail, the two primeval stands were sampled in the Ukrainian relic virgin beech forest of Uholka (Trotsiuk et al., 2012), the ten planter–old-growth and old-growth stands were sampled in the strict forest Reserves of Valle Cervara and Sasso Fratino (respectively in Abruzzo, Lazio and Molise National Park, and Foreste Casentinesi National Park; Italy), and the other forest stands were sampled in three Italian protected areas (Sibillini National Park, Foreste Casentinesi National Park, Torricchio Strict Nature Reserve) as well as among the Italian forest monitoring network sites (CON.ECO. FOR., Petriccione and Pompei, 2002).

CD exhibited a significant U-shaped pattern over time, with early successional stages and primeval forests displaying higher diversity of plant species combinations (Fig. 2).

In recently logged, open-canopy forests (0–30 years), species richness was notably high. Widely recognized across diverse forest ecosystems, recent disturbances trigger a temporary surge in available resources. In these forests, this surge results in heightened light availability, accelerated organic decomposition, and improved nutrient availability within the forest stand (Chelli et al., 2023). Some plants, typically fast-growing and quick to colonise competitive and ruderal plants (Grime et al., 1997), capitalise on this short-term resource pulse. During these initial stages, it is also not uncommon for species from neighbouring vegetation types, such as grasslands, to establish a presence, at least temporarily (Bartha et al., 2008). Consequently, CD was also high, likely influenced by the recent disturbance, which reduced interspecific competition and favoured diverse species combinations (Barkham, 1992).

The decline of species richness and CD in the second stage of forest succession (30–70 years) has been empirically linked to structural changes in the tree canopy layer observed in temperate forests (Chelli et al., 2023). This transitional phase marks progressive canopy closure and thickening, signalling the end of the resource pulse characterising early successional stages. These subtle declines in resource availability (i.e., light [energy] and nutrients) result in a reduction in competitive and ruderal species, allowing for the establishment of species better suited to these conditions (i.e., specialist species; Hofmeister et al., 2022; Chelli et al., 2023). However, a notable decoupling between the two diversity measures occurred after 300 years of forest succession, as evidenced by non-overlapping error bars (Fig. 2). In old-growth (>300 years) and primeval forests, species richness remained relatively low and stable, contrary to what was found by Hilmers et al. (2018). This
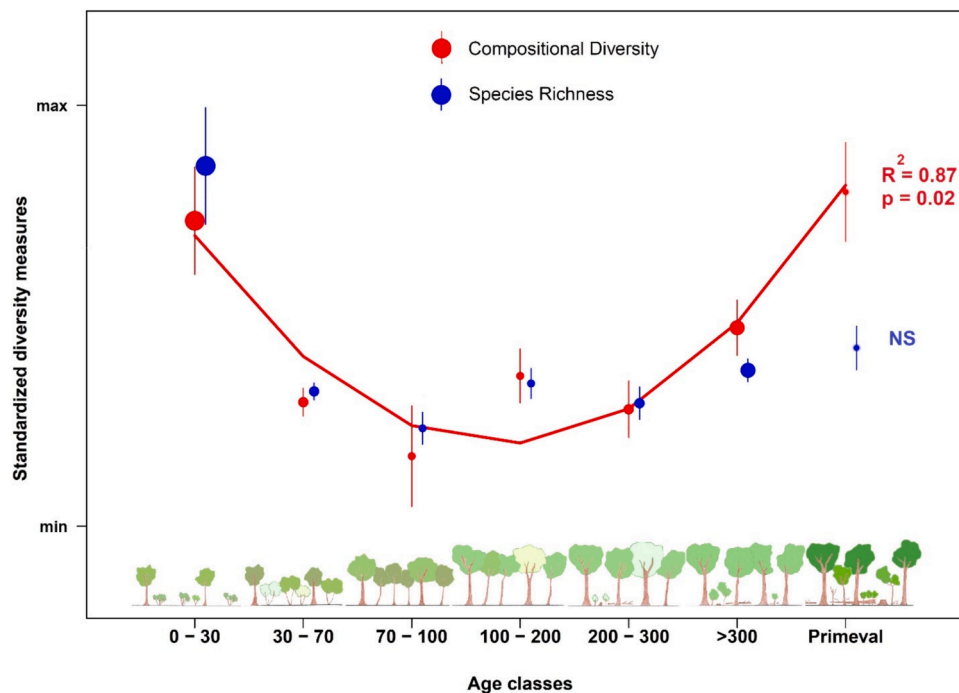
Fig. 2. The standardised (using the 'scale' R function) mean value of Compositional Diversity (CD; in red) and species richness (in blue) from 30 forest stands positioned across forest successional classes (modified from Hilmers et al., 2018). The size of the circles increases along with the number of the stands used to calculate the age class mean value and range from smallest (n = 2) to largest (n = 8); the solid lines reported for each class represent the standard error of the diversity measure. The R^2 and p-value of quadratic regressions are reported. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

probably depends on the fact that our succession lacks open-canopy forests in terminal and decay classes. Unlike species richness, CD showed an increasing trend, reaching its peak in primeval forests. This pattern suggests that centuries of uninterrupted forest development favour a select group of late-successional species. Not only the number of these species remains constant (see Fig. 2), but the species composition shows no significant differences between stages of forest succession (Appendix S1). Overall, these results point to the fine-scale re-arrangement of the similar number and identity of species, contributing to more diverse assemblages in old-growth and primeval forests compared to younger forests (Bartha et al., 2020).

Regarding the spatial scale at which the maximum CD is reached, we demonstrate that it is lower in both young forests (0–30 years; 0.85 m²) and old-growth forests (>200 years; 0.45–0.78 m²; Appendix S2). In young forests, the high diversity of species combination at low spatial scale is likely generated by recent disturbances (i.e., logging), while in old-growth and primeval forests, this pattern is probably supported by the fine-scale spatial heterogeneity of resources, including light, nutrients, and moisture (Bartels and Chen, 2010). However, the challenge of identifying underlying mechanisms leading to those patterns remains open. Null models should be applied to separate random, intraspecific and interspecific effects to assist in detecting and interpreting the spatial associations between species and environment (Podani, 1984; Dale and Fortin, 2014). For example, Bartha et al.'s (2020) research from beech forests used null models to establish that patterns of beta diversity in old-growth forests were a product of microhabitat availability for late-successional species.

5. Conclusion

The adoption of diversity measures that shed light on species interactions holds major implications for conservation and restoration ecology, enriching the debate on the selection of effective indicators of sustainable forest management (SFM; Forest Europe, 2020). Firstly,

considering the current state of Europe's forests, predominantly in intermediate stages due to extensive exploitation in the early 20th century and subsequent abandonment (Hilmers et al., 2018), it is suggested to emphasise the protection of both under-represented old-growth and primeval European forests (Ahlström et al., 2022) and the early-successional forests (Swanson et al., 2011). The former forests are fundamental for safeguarding their unique within-community species assemblages, often not reflected in high alpha diversity. The latter may play a role in conserving high levels of plant species richness, especially where the protection of non-forest, light-demanding species holds local priority (see Kopecký et al., 2013).

Secondly, restoring the understorey plant species assemblages of a forest to a complex, close-to-nature state necessitates a time scale (i.e., > 200–300 years) distinct from merely restoring alpha diversity. The process of reinstating the number and fine-scale spatial configuration of plant species combinations that naturally occur in a forest demands more time and effort than simply restoring species count, thus encouraging ecologists to extend the time span of their chronosequences for studying forest successions. This phenomenon likely stems from the heightened sensitivity of species assemblages to forest structure compared to species richness (Burrascano et al., 2018; Thompson et al., 2022), an aspect which deserves further studies.

Thirdly, since within-community species combinations offer insights beyond alpha diversity, especially beyond the 200–300-year mark, they serve as a valuable plant diversity indicator for forest management planning and restoration monitoring, especially to assess whether a given forest has reached old-growth characteristics (Bartha et al., 2004; McCallum et al., 2018; Bartha et al., 2020).

Lastly, further research endeavours should delve into species interactions (e.g., combinations types resulting from competition or facilitation) and functional traits to unravel how species with divergent life history strategies interact and coexist within assemblages, revealing taxonomic and functional-based patterns. Ideally, these future investigations should consider expanding the number of sampling sites

along the successional gradient – especially the number of primeval forests – and evenly distributing them among age classes, aspects that limit our study.

CRediT authorship contribution statement

Stefano Chelli: Writing – original draft, Conceptualization. **James Lee Tsakalos:** Writing – original draft, Conceptualization. **Zhengxue Zhu:** Writing – review & editing, Formal analysis, Data curation. **Luciano Ludovico Maria De Benedictis:** Writing – review & editing, Formal analysis, Data curation. **Sandor Bartha:** Writing – review & editing, Validation. **Roberto Canullo:** Writing – review & editing, Investigation, Funding acquisition. **Liubov Borsukevych:** Writing – review & editing, Investigation. **Marco Cervellini:** Writing – review & editing, Investigation. **Giandiego Campetella:** Writing – review & editing, Supervision, Project administration.

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.

Data availability

Data will be made available on request.

Author contributions

S.C., J.L.T., and G.C. conceived the idea. J.L.T., Z.Z, and L.L.M.D.B. performed the analyses. S.C. and J.L.T. wrote the first draft of the manuscript. All co-authors contributed to the critical revision of the manuscript to produce the final version.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112089.

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