# A spatially explicit index for tree species or trait diversity at neighborhood and stand level

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## ABSTRACT

Knowledge about tree species interactions is important for our understanding of forest ecosystems. Research about such interactions requires a quantitative description of different stand mixture types for example with measures of species- or trait-diversity like Simpson- or Rao-diversity. Many currently available diversity measures are based on relative proportions and do not account for the spatial configuration of a stand. They implicitly assume that all trees are equally likely to interact with one another, irrespective of their spatial distance. However, fundamental ecosystem processes such as competition are strongly influenced by intra- or interspecific interactions that take place between neighboring trees.

This study introduces a measure for the neighborhood diversity (NDiv) around individual trees by averaging the dissimilarity between a tree and all its neighbors. NDiv uses maps of the 'area potentially available' to trees (APA) to define tree neighborhoods. APA-maps are derived by spatially dividing the entire stand area into adjacent patches that approximate the growing space that is potentially available to each tree. The average NDiv of all trees of a stand weighted by the sizes of their APA-patches provides a consistent diversity measure at stand-level. Depending on the used dissimilarity measure, NDiv may either quantify species or trait neighborhood diversity. Species neighborhood diversity and tree height neighborhood diversity of case-study plots were analyzed to demonstrate the application of NDiv.

When tree locations were spatially randomized in a simulation study, NDiv of the case-study plots at stand-level was nearly identical to Simpson-diversity. However, the actually observed NDiv of plots with patch-wise mixing of tree species was considerably lower than their Simpson-diversity. On these plots, NDiv accounted for a limited potential for interactions among species since the tree species were growing spatially separated in patches.

NDiv is a useful measure of tree diversity when trees are not randomly distributed across a stand and when mixing effects mainly derive from interactions between neighboring trees. The use of NDiv as explanatory variable may help to account for the spatial configuration of trees in forests which may increase the explanatory power of analyses of relationships between tree diversity and ecosystem processes.

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**Box 1**
Terminology related to tree species and traits.

Species- and trait diversity are two of the most prominent approaches to assess tree diversity. The methods described here to assess diversity use as well information about species- or trait-dissimilarity between trees but they additionally account for the spatial configuration of stands. The term 'tree trait' is used synonymously with 'properties that occur at the individual tree level or lower' (Violle et al., 2007; e.g. basal area, tree height, leaf size). As species dissimilarity is calculated identically to trait

dissimilarity using a single categorical trait, it is mostly not necessary to differentiate further between both dissimilarity measures for this study. When referring to 'traits', 'trait composition' and 'trait diversity', 'species', 'species composition' and 'species diversity' are always implicitly included.

## 1. Introduction

Trees in forest stands are interacting with other trees in their direct surroundings through various mechanisms. For example, strong

competitors may profit from an advanced access to resources such as light or water with increased tree growth or a reduced mortality (Fichtner et al., 2012; Ruiz-Benito et al., 2013; Metz et al., 2020). Besides size differences of competing trees, species identity of neighbors may have an influence on tree processes (Forrester and Bauhus, 2016). Facilitative interaction between trees may occur when a tree profits from additional resources that are provided by its neighbors. For example, this can be the case with nitrogen fixing neighboring trees (Forrester et al., 2006) or when deep-rooting neighbors lift water from lower soil layers to the topsoil (Zapater et al., 2011; Hafner et al., 2017).

Some of the mechanisms that are responsible for the relationship between forest biodiversity and stand-level ecosystem processes such as productivity take place at the neighborhood-level (Forrester and Bauhus, 2016). For example, complementary crown shapes of neighboring trees may lead to a higher light interception and productivity due to higher canopy space filling (Pretzsch, 2014; Ammer, 2019). Light use strategies of differently sized trees may lead to overyielding at the stand-level, when small and large tree are mixed (Madrigal-González et al., 2016).

The spatial configuration of forest stands does have a large impact on the composition of the neighborhoods of trees. In a forest stand with stem-wise mixing of tree species, trees have a higher proportion of neighbors of another species than in stands with patch-wise mixing, even if relative proportions of all tree species are identical. A different potential for direct interaction between trees of different species depending on the spatial pattern of a stand may have an impact on some stand-level processes. As many common indices for species or trait diversity at stand-level do not account for its spatial configuration (e.g., species richness, Simpson- or Rao-diversity; Simpson, 1949; Rao, 1982), they may not be able to capture the actual potential for interaction between different trees. Therefore, spatially explicit indices for species and trait diversity measures that may be used as covariables when analyzing the response of stand-level processes (e.g., productivity) on biodiversity are necessary to develop a better mechanistic understanding of ecosystem functioning.

To analyze how stand-level processes respond to the spatial configuration of trees, the spatial information has to be aggregated at stand-level first. Even though the study of the spatial configuration of forest stands is a very active field of research (for example using point pattern analysis; Perry et al., 2006; Wiegand et al., 2013; Velázquez et al., 2016), not all spatial summary statistics are suitable to be used to explain responses of ecosystem processes. Many spatial summary statistics derived from point pattern analysis are functions of a focal distance (e.g., Ripley's K or the pair correlation function; Ripley, 1976; Illian, 2008). Even though diagrams about how a spatial summary statistic changes with focal distance is highly informative for an understanding of the spatial structure of a forest stand, a transformation of such distance dependent summary statistics into stand-level characteristics is not straightforward. Many stand-level indices that quantify the spatial configuration of a stand provide useful information about general spatial patterns of trees such as spatial clustering (e.g., Clark and Evans, Morisita's Index of dispersion, uniform angle index) but they do not consider differences between species.

One approach to describe the spatial configuration of tree species with stand-level variables is to estimate the species diversity in the neighborhood of trees first (e.g., using nearest neighbor statistics) and then to upscale from the neighborhood- to the stand-level using appropriate aggregation functions (Hui et al., 2011; Gadow et al., 2012; Yang and Man, 2018). As a large variety of tree-level processes and tree traits are related to neighborhood characteristics (Fichtner et al., 2013; Chen et al., 2016; Juchheim et al., 2017; Grossman et al., 2019; Fan et al., 2020), the average diversity of tree neighborhoods is a promising approach for the design of spatially explicit diversity indices at stand-level. Usually, estimating neighborhood diversity at stand-level is a three step procedure. First, a method to select neighbors of a focal tree has to be found. After that, the species diversity of the neighborhood

structure has to be estimated. Lastly, an aggregation function has to be chosen that upscales neighborhood diversities to the stand-level.

### 1.1. Selecting neighbor trees

Selection of neighbors is usually either done by choosing a pre-defined number of nearest neighbors (e.g., Aguirre et al., 2003; Yang and Man, 2018; Hui et al., 2019), by selecting all trees in a fixed radius around focal trees (Chen et al., 2016; Fan et al., 2020) or by choosing trees based on the size of the focal tree and its potential neighbors (e.g., by overlapping crown projection areas - Ratcliffe et al., 2015). All these approaches have a limited flexibility as they only consider distances between a focal tree and its potential neighbors and not the specific spatial configuration of the forest stand around trees. For example, a large tree that is standing in between two other trees may present a barrier and thus prevent interaction between trees that otherwise would be direct neighbors. A highly flexible neighborhood definition that is capable of considering the complete spatial configuration around focal trees was introduced by Abellanas et al. (2016). This neighborhood definition is based on tessellated maps where the complete stand area is separated into adjacent patches that approximate the share of growing space and resources that is potentially available to individual trees (maps of the 'area potentially available to trees', APA, Gspaltl et al., 2012; Dirnberger and Sterba, 2014; Dirnberger et al., 2017; Fig. 1 and Figure S1, see the methods section for a more detailed description of the generation of APA-maps). In contrast to crown-maps that illustrate the approximate area of a plot that is covered by the crown projection of a tree, the structure of APA-maps is similar to rasterized landscape maps of different land cover classes (only on a much finer scale, Fig. 1). Each APA-patch approximates the location and shape of the region in 2D-space that is dominated by a particular tree. This complete tessellation of the stand area permits defining two trees whose APA-patches share a common border as neighbors (Abellanas et al., 2016).

### 1.2. Estimating diversity at neighborhood-level

After a neighborhood structure that is composed of a focal tree and its neighbors is defined, its diversity needs to be estimated. For example, neighborhood diversity may be estimated as the overall diversity of all neighbor trees (e.g., Shannon diversity of all neighbor trees - Ratcliffe et al., 2015; number of different tree species in a tree neighborhood - Fichtner et al., 2017). Another approach to estimate neighborhood diversity is by averaging the dissimilarity between all pairs of the focal tree and each of its neighbors (e.g., proportion of neighbor trees with a different species than the focal tree, tree species mingling – Gadow, 1993; Aguirre et al., 2003; Hui et al., 2019; weighted average trait dissimilarity - Chen et al., 2016). Sometimes a mix of both is applied (Hui et al., 2011).

Some neighborhood indices treat all neighbors equally (e.g., Aguirre et al., 2003; Ratcliffe et al., 2015; Fichtner et al., 2017). However, as large neighbor trees and neighbor trees in close distance to one another have a stronger potential to interact (Uriarte et al., 2004), it may be more realistic to differentiate between neighbors of a focal tree depending on their size and position (Chen et al., 2016).

Additionally, trait-based approaches to estimate forest diversity are being applied more frequently, as they are capable of differentiating better between similar and dissimilar tree species (Nadrowski et al., 2010; Chen et al., 2016). To keep up with this development, neighborhood diversity indices should be flexible enough to support trait based approaches as well.

### 1.3. Upscaling to stand-level

Lastly, an appropriate function to upscale neighborhood diversities to the stand-level has to be selected. Some studies propose to use the ordinary arithmetic mean of the neighborhood diversity of all trees to
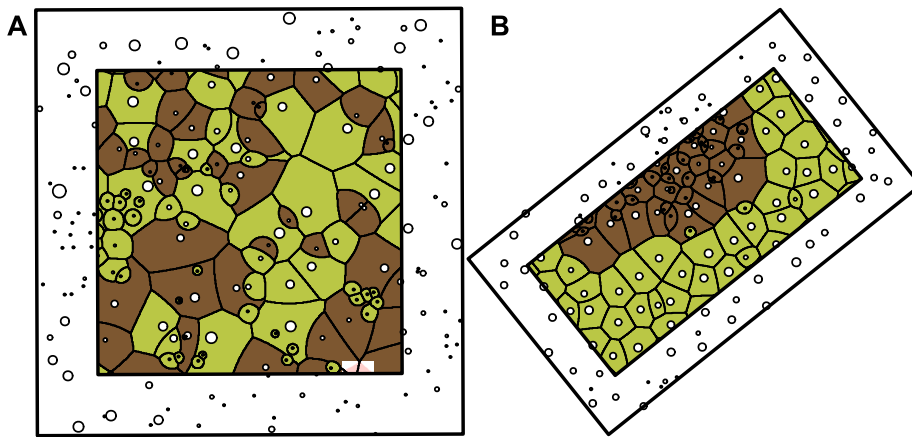
**Fig. 1.** Examples of maps of the 'area potentially available' (APA-maps) from two case-study plots from Germany (A: 5.2, B: 8.2, see Methods section for a plot description). Brown patches are the APA of European beech *(Fagus sylvatica)* trees. Purple patches refer to the APA of Douglas-fir trees *(Pseudotsuga menziesii)*. Points mark tree locations. Point radii are proportional to the tree diameter at breast height. The stand in a 10 m buffer zone (white area) around the actual core plot (colored patches) was included into the calculation of the APA-maps to avoid edge-effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

estimate species- or stand-level neighborhood diversity (e.g., segregation index of Pielou, 1977; tree species spatial diversity of Hui et al., 2011; stand mean neighborhood species diversity of Yang and Man, 2018). However, large trees usually have access to more resources than small trees and their influence on ecosystem processes at stand-level is higher. When upscaling neighborhood diversity to the stand-level, some measure of tree size should be included as weighting factor.

### 1.4. Study goals

Three major points were identified that should be considered when quantifying neighborhood diversity of trees and methods for upscaling to the stand level.

- **Neighborhood definition and weighting:** Whether two trees have a high or low potential for interaction depends on the distance between them, their size and the size and position of other competing trees in their neighborhood. Selection of neighboring trees and the weight each neighbor has on the estimation of the neighborhood diversity of a focal tree should be adjusted accordingly.
- **Support for trait based diversity measures:** It should be possible to use different sets of categorical, ordinal and numerical variables to describe the diversity of tree neighborhoods.
- **Considering tree size when upscaling:** Large trees may have a greater influence on ecosystem processes than small trees. When upscaling from neighborhood-level to stand-level, the neighborhood diversity of large trees should be weighted higher than the one of small trees.

Currently, there are no methods available to estimate average diversity of tree neighborhoods in forest stands that take all of these three points into account. Therefore, the goal of this study is to introduce a new index for neighborhood diversity (NDiv) and upscaling methods for the stand-level that use spatial information from APA-maps to overcome previous limitations of neighborhood analyses. As computational complexity may be one of the reasons why APA-maps have not been used more frequently in the past, software for the calculation of APA-maps and NDiv is provided via the APAtree-package (Glatthorn, 2021) for the R-software (R Core Team, 2021). The use of NDiv may support an accurate description of the actual potential for interaction between trees of different species and with different traits when analyzing relationships between forest biodiversity and other ecosystem features.

### 2. Materials and methods

The neighborhood diversity of an individual tree is defined as the average dissimilarity between the tree and all its neighbors. The potential for interaction between two trees depends on the distance

between the trees, on their size and as well on the position and size of other competitors in the neighborhood. The approach presented here approximates the potential for interaction between two trees with the relative border lengths between APA-patches of a focal tree and all its neighbors (Fig. 2). As all diversity estimations later are based on APA-maps, their generation is explained first.

### 2.1. Mapping of the area potentially available

APA-maps of a forest stand (consisting of N trees) are derived from a rasterized 'Multiplicatively Weighted Voronoi Diagram' of the overall plot area (Gspaltl et al., 2012; Römisch, 1995) (Fig. 2 A). This method rasterizes the plot region into a regular rectangular grid (consisting of M grid cells) and maps a tree to each grid cell $c_m (m \in \{1, 2, \cdots, M\})$ using the function

$$Tree(c_m) = \underset{t_i}{argmin}[d(c_m, t_i)/w_i] \qquad 1$$

where $d(c_m, t_i)$ is the distance between grid cell center and tree $t_i$ and $w_i$ is a weighting factor that accounts for the competitive ability of a tree $(i \in \{1, 2, \cdots, N\})$. If Equation (1) returns more than one tree for a cell, one of the trees is randomly selected to ensure a unique assignment of individual trees to grid cells (e.g., if a grid cell center happens to be in
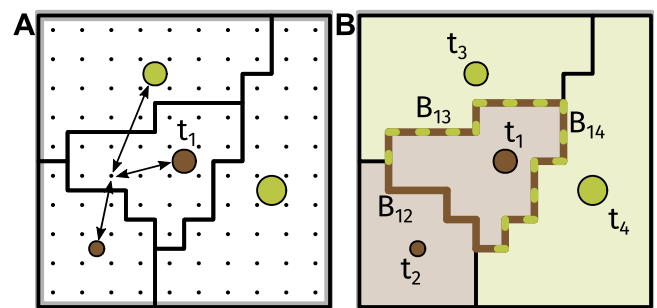


**Fig. 2.** Panel A: Generation of a map of the 'area potentially available' to trees (APA-map) via a rasterized 'Multiplicative Weighted Voronoi Diagram' (MWVD). Trees (large points) are assigned to all grid cells by minimum distance (arrows) between grid cell center (small points) and tree, weighted by the competitive ability of the trees. Point radii are proportional to the trees competitive ability (e.g., approximated with the crown radius). The APA-patch of the center tree $t_1$ (APA$_1$) consists of the 18 grid cells to which this tree was assigned. Panel B: Calculation of the species diversity of the neighborhood of a tree (SpeciesNDiv$_i$). SpeciesNDiv$_i$ of the center tree is the relative proportion of the combined border lengths of the mixed borders (dashed) to the overall border length of the tree (solid and dashed combined). A more detailed explanation that includes as well a trait-based version of NDiv and upscaling methods to the stand-level is given in the main text.

the exact middle between trees with equal competitive ability). Effects of this random selection on results can be minimized by a sufficiently fine grid resolution. In most cases, the actual competitive ability will be hard to estimate and has to be approximated for simplicity with measurable tree traits (e.g., diameter at breast height - DBH, crown radius, leaf area).

The APA-patch of a tree (Fig. 2 A) is defined as the set of all grid cells to which this tree was assigned:

$$APA_i = \{c_m | Tree(c_m) = t_i\} \qquad 2$$

Please note that $APA_i$ refers to the set of grid cells that delineates location and shape of the APA-patch of tree i in two-dimensional space and not an area size. The area size of an APA-patch is given by the total number of grid cells that are assigned to one tree multiplied with the squared resolution (res) of the grid

$$APAsize_i = |APA_i| res^2. \qquad 3$$

As the calculation of neighborhood diversities is based on border lengths between APA-patches, these borders and their lengths need to be described. Each grid cell $c_m$ is the subset of all points P in a stand that are in half the resolutions distance or closer from the grid cell center in × and y direction

$$c_m = \left\{ P \left| \frac{dist_x(center(c_m), P) \le 0.5res\&}{dist_y(center(c_m), P) \le 0.5res} \right. \right\} \qquad 4$$

The union of all grid cells of one APA-patch ($\bigcup APA_i$) represents all points in a stand that are assigned to a particular tree. The border between two trees i and j consists of all points that are shared between their APA-patches

$$B_{ij} = \{ \cup APA_i \} \cap \{ \cup APA_j \}; i \ne j. \qquad 5$$

The length of border $B_{ij}$ is denoted by $BL(B_{ij})$. Two trees are neighbors if their shared border length $BL_{ij}$ is greater than zero. Two trees are no neighbors if their APA-patches do not share any points (i.e., if $B_{ij}$ is empty with $BL_{ij} = 0$).

### 2.2. Neighborhood diversity at individual tree level (NDiv_i)

The neighborhood diversity of an individual tree i is given by the average dissimilarity $D_{ij}$ between a tree and its neighbors weighted by their shared border lengths:

$$NDiv_i = \frac{\sum_{j=1}^{N} BL_{ij} D_{ij}}{\sum_{j=1}^{N} BL_{ij}}; i \ne j. \qquad 6$$

As the border length between non-neighboring trees is zero anyways, there is no need to specify an index that refers to neighboring trees only. In its most basic form, dissimilarity $D_{ij}$ is zero if trees i and j are of the same species and one if species are identical:

$$D_{spec.ij} = \begin{cases} 0 \text{ if } species_i = species_j \\ 1 \text{ otherwise} \end{cases} \qquad 7$$

In this case, $NDiv_i$ is simply the relative proportion of mixed borders that a tree shares with its neighbors (Fig. 2 B). When using a trait-based approach, an appropriate measure for trait-dissimilarity has to be selected in Equation (Pavoine et al., 2009; Bello et al., 2013). In this study the univariate Gower distance

$$D_{trait.ij} = \sqrt{\frac{|trait_i - trait_j|}{range(trait)}} \qquad 8$$

is used to calculate $NDiv_i$ exemplarily (Gower, 1971; Pavoine et al., 2009), where range(trait) is the difference between the minimum and maximum trait value of all sampled trees. $NDiv_i$ is highly flexible

regarding the way how dissimilarity between trees is assessed. Which uni- or multivariate dissimilarity measure should be used always depends on the specific research question at hand.

### 2.3. Upscaling neighborhood diversity to species and stand-level

Upscaling of $NDiv_i$ to species and stand-level is done by averaging over all trees of the same species or of the complete stand. However, as the contribution of a large tree to species- or stand-level processes is mostly greater than the one of a small tree, a weighted mean that considers tree size is more appropriate than an ordinary mean. To upscale $NDiv_i$, the size of the APA-patch of a tree ($APAsize_i$) is used as weighting factor.

$$NDiv_k = \sum_{i|species_i=k} [NDiv_i APAsize_i] / \sum_{i|species_i=k} [APAsize_i] \qquad 9$$

quantifies the average neighborhood diversity of all trees that belong to species k (out of the total number of species S), whereas

$$NDiv_{stand} = \sum_{i=1}^{N} [NDiv_i APAsize_i] / \sum_{i=1}^{N} [APAsize_i] \qquad 10$$

is the average neighborhood diversity of the complete stand.

Using relative proportions of trees

$$p_i = \frac{APAsize_i}{\sum_{j=1}^{N} APAsize_j} \qquad 11$$

and species

$$p_k = \sum_{i|species_i=k} p_i. \qquad 12$$

$NDiv_k$ and $NDiv_{stand}$ may be further simplified to

$$NDiv_k = \sum_{i|species_i=k} [NDiv_i p_i] / p_k \qquad 13$$

and

$$NDiv_{stand} = \sum_{i=1}^{N} NDiv_i p_i = \sum_{k=1}^{S} NDiv_k p_k. \qquad 14$$

$NDiv$ is defined for multiple organizational levels (tree-, species- and stand-level) and supports different approaches to consider dissimilarity between trees. This is a great strength of the index. However, this flexibility makes it necessary to label $NDiv$ carefully with a prefix that defines the traits that have been used to assess the dissimilarity between trees (e.g., SpeciesNDiv, HeightNDiv) and a subscript that refers to the level of organization (e.g., $NDiv_{stand}$) to prevent misunderstandings (Fig. 3). The R-functions that have been developed to create and analyze APA-maps is provided via the APAtree-package (Glatthorn, 2021) for the R-software (R Core Team, 2021). All raw data, data processing and data analysis is documented in the APAtree package.

## 3. Relationship between NDiv and conventional diversity measures

The approach how NDiv quantifies diversity resembles the concepts of some common conventional diversity measures that do not consider the spatial configuration of a community. For example, Simpson diversity

$$SD = \sum_{i=1}^{N} p_i \sum_{i=j}^{N} D_{species,ij} p_j = 1 - \sum_{k=1}^{S} p_k^2 \qquad 15$$

is defined as the probability to select trees of a different species when randomly drawing two trees from a population (Simpson, 1949). The

$$Prefix\underbrace{\textbf{\textit{NDiv}}}\underbrace{\textit{subscript}}$$

**Dissimilarity measure:**

***Species***-dissimilarity (equation X)

***Trait***-dissimilarity (equation X)

**Organizational-level:**

Tree-level (equation XXX):
***i, j, 1:*** neighborhood diversity of any tree (i or j) or of a specific tree (e.g., tree number 1)

Species-level (equation XXX):
***k, beech:*** average neighborhood diversity of all trees of a species

Stand-level (equation XXX):
***stand:*** average neighborhood diversity of all trees of a stand

**Fig. 3.** Labelling of the neighborhood diversity index NDiv. As NDiv is highly flexible regarding the used dissimilarity measure (prefix) and the organizational level (subscript) to estimate neighborhood diversity, it has to be labelled carefully to avoid confusion. Dissimilarity measure and organizational level may be combined freely. For example, SpeciesNDiv$_{beech}$ assesses the average species diversity in the neighborhood of beech trees. HeightNDiv$_{stand}$ is the average height diversity in the neighborhood of all trees of a stand.

selection probability of a tree is usually weighted by its relative proportion to estimate forest diversity. In a similar way, SpeciesNDiv$_{stand}$ may be interpreted as the probability to randomly select two trees of a different species when randomly drawing a pair of neighboring trees.

A more general extension of Simpson diversity that is based on trait dissimilarity is Rao diversity

$$RD = \sum_{i=1}^{N} p_i \sum_{j=1}^{N} D_{trait,ij} p_j, \qquad 16$$

which is defined as the average dissimilarity between two randomly drawn individuals (Rao, 1982). If Rao-diversity is estimated using species-level trait averages that ignore differences between individuals of the same species, Rao diversity may be calculated as well based on relative species proportions and a species by trait dissimilarity matrix (Botta-Dukát, 2005; Laliberté and Legendre, 2010).

If all trees are randomly distributed across a stand, average species dissimilarities between neighboring trees (SpeciesNDiv$_{stand}$) will be approximately identical to the average dissimilarities between all trees in a stand, which is the definition of Simpson diversity (see results section). A corresponding diversity measure that does not account for the spatial configuration and only uses relative proportions may be calculated for every way to specify NDiv (Fig. 3). If trees are randomly distributed across the stand, NDiv is always approximately identical to this counterpart that ignores the spatial configuration is based on relative area proportions only (PDiv), which describes the average dissimilarity between a tree and all other tees in a stand:

$$PDiv_i = \sum_{j=1}^{N} D_{ij} p_j. \qquad 17$$

PDiv$_i$ describes the proportion-based diversity at the individual tree level. Proportion-based diversity measures at species- and stand-level are obtained by substituting NDiv$_i$ in Equations (9) and (10) with PDiv$_i$ (Equation (17)). For example,

$$SpeciesNDiv_{stand} = \sum_{i=1}^{N} SpeciesNDiv_i p_i \qquad 18$$

simplifies for random tree distributions approximately to

$$SpeciesPDiv_{stand} = \sum_{i=1}^{N} SpeciesPDiv_i p_i = \sum_{i=1}^{N} p_i \sum_{i=j}^{N} D_{species,ij} p_j \qquad 19$$

which is equivalent to Simpson diversity (Equation (15)). The corresponding abundance based diversity of TraitNDiv$_{stand}$ is Rao-diversity.

### 3.1. Spatial segregation of similar trees

NDiv merges information about the spatial configuration of a stand and about the diversity of the trait composition of the trees into a single index. For studies that are interested in an overall quantification of diversity this may be suitable. If the study objective requires it to address the spatial configuration of a stand and its diversity independently, it is better to differentiate between the spatial configuration and the proportion-based diversity (PDiv) of a stand using two separate indices that are unrelated. This is done by calculating a 'segregation-index (seg)' of NDiv that quantifies how much NDiv deviates from its random expectation. This is similar to the approach used by Pommerening and Uria-Diez (2017), who calculated a species segregation index based on the ratio between a nearest neighbor index (species mingling M) and its random expectation. To estimate the random expectation of NDiv, random tree distributions are simulated by randomly choosing new x- and y-coordinates for each tree. Each location within the plot area is equally likely to be selected (complete spatial randomness). The segregation-index of NDiv [seg(NDiv)] is defined as the number of standard deviations that the observed NDiv$_{obs}$ is deviating from its random expectation NDiv$_{exp}$:

$$seg(NDiv_{obs}) = (NDiv_{obs} - NDiv_{exp})/s(NDiv_{exp}) \qquad 20$$

This way to account for the variance of a random simulation is inspired from a randomization approach used by Gotelli and McCabe (2002) for species presence-absence matrices. The random relocation of the tree coordinates will not only have an effect on the diversity of tree neighborhoods but as well on the size of the APA-patches of the trees. As PDiv is estimated using relative area proportions, NDiv and PDiv will both be influenced by the random simulations. Due to a strong relationship between simulated NDiv- and PDiv-values (e.g., SpeciesNDiv$_{stand}$ to Simpson diversity, Fig. 4), the simulated PDiv-values have to be considered when calculating NDiv$_{exp}$ and s(NDiv$_{exp}$) when estimating seg(NDiv). This is done by using a standard linear regression model that relates the simulated NDiv-values (NDiv$_{sim}$) to the simulated PDiv-values (PDiv$_{sim}$; Fig. 4). The expectation value (E) and the standard deviation (s) of the linear model prediction, conditional on the observed PDiv-value (PDiv$_{obs}$), are then used to estimate

$$NDiv_{exp} = E[NDiv_{sim}|PDiv_{obs}] \, and \qquad 21$$

$$s(NDiv_{exp}) = s[NDiv_{exp}|PDiv_{obs}] \qquad 22$$

Values of seg(NDiv) larger than zero indicate a dispersed distribution of similar trees, whereas values below zero indicate aggregation of similar trees at the neighborhood-level. Proportion-based diversity
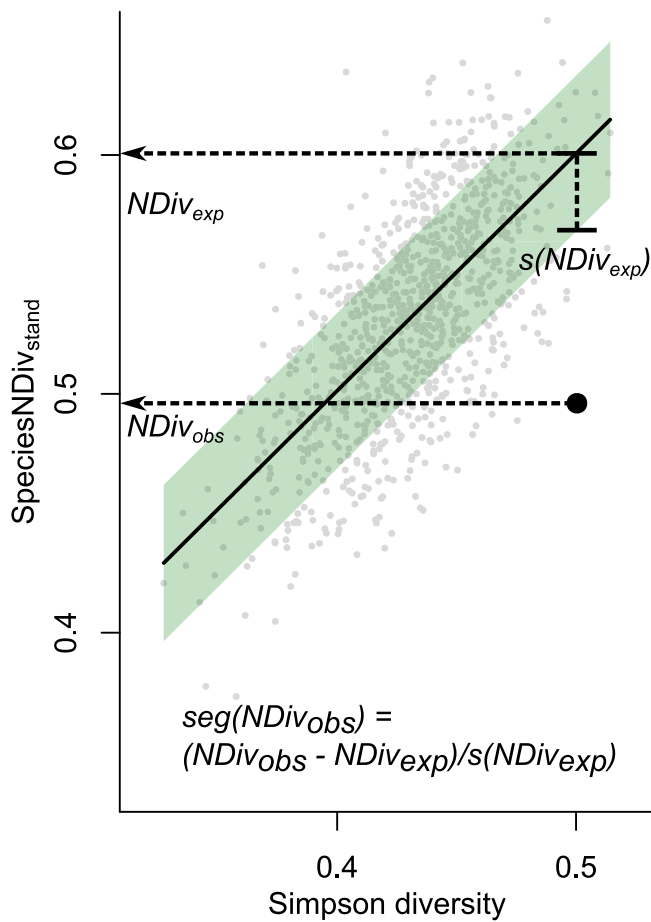
**Fig. 4.** Calculation of the 'segregation index (seg) of the species neighborhood diversity of a forest stand (SpeciesNDiv$_{stand}$ of plot 4.2 of the case-study). If tree species are distributed randomly across the entire plot area, SpeciesNDiv$_{stand}$ is approximately identical to Simpson diversity. This is on average the case for 1000 simulations of the stand, where tree positions were completely spatially randomized (gray points). Even though Simpson diversity is a proportion-based diversity measure, it is calculated here based on the sizes of APA-patches, which change when tree coordinates are shifted. The segregation index quantifies the relative difference between the observed NDiv value (NDiv$_{obs}$) and its random expectation (NDiv$_{exp}$). In this example, seg(SpeciesNDiv$_{stand}$)is −3.18, which indicates that in the neighborhood of all trees there are on average fewer trees of different species than would be expected from a random distribution of tree species (i.e., tree species grow in patches in this stand). The black line and the green band represent the regression line and its standard deviation of a standard linear regression between the simulated NDiv-values and the simulated Simpson diversity values. Using this model, NDiv$_{exp}$ and s(NDiv$_{exp}$) are the conditional mean and the conditional standard deviation, given the observed Simpson diversity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measures such as Simpson or Rao diversity may be used together with seg(NDiv) in multivariate analyses about the relationship between forest diversity and other ecosystem characteristics.

### 3.2. Case-study

The introduced methods are demonstrated by using case-study sites from Lower Saxony, Germany (geographic range: 9.26° E to 10.84° E and 51.66° N and 53.2° N). The sixteen plots (Table 1) are part of a project that addresses ecosystem functioning of different tree species mixtures. The plots consist either of European beech (Fagus sylvatica L.) and Norway spruce (Picea abies L. KARST) or European beech admixed with Douglas-fir (Pseudotsuga menziesii MIRB. FRANCO).

Each plot consists of a rectangular core plot with a size of 0.25 ha and a buffer zone of 10 m around the plots (plus-sampling, Fig. 1). All living trees with a DBH greater or equal than 7.0 cm were mapped within the buffer zones (1339 trees in total on all plots) and the core zones of the plot (1474 trees in total) with the Field-Map system (Field-Map, IFER, Czech Republic). Tree coordinates, DBH and species were recorded for every tree. Tree height was measured with a Vertex IV (Haglöf, Langsele, Sweden) or a laser height meter (TruPulse Laser 360 R, Laser Technology Inc, Centennial, USA) for a subset of in total 112 trees in all 16 core plots together. The remaining tree heights were estimated with predictions from non-linear mixed effect models (Mehtätalo et al., 2015). General data about the plots and from the tree inventory has been uploaded to the PANGAE archive (Ammer et al., 2020).

To approximate the competitive ability of trees for the generation of APA-maps of the case-study plots, the 95 % quantile of the crown radius of trees CR$_{95}$ was used. The CR$_{95}$ was allometrically estimated from the trees DBH with species-specific allometric equations provided by Pretzsch et al. (2015). These equations approximate the upper crown radius that a tree of a certain DBH can reach. The selection of CR$_{95}$ is based on the assumption that the upper distance at which a tree of a certain DBH is capable of supporting leaves is a good approximation of the aboveground competitive ability of trees. Use of the CR$_{95}$ is preferred over the crown projection area (π CR$_{95}^2$) because it better fits to the assumption of a linear decline of the competitive ability of a tree with distance.

Two different NDiv-variables and their corresponding proportion-based counterparts were calculated from the case-study plots:

- SpeciesNDiv$_{stand}$ – the 'average species neighborhood diversity'. That is, the average share of trees of a different species in the neighborhood all trees of a stand (Equations (10) and (7));
- SD – Simpson diversity according to the APA-size proportions of all tree species of a stand (Equations (15) and (7));
- HeightNDiv$_{stand}$ – the 'average height neighborhood diversity of a stand'. That is, the average dissimilarity of tree heights between all trees of a stand and their direct neighbors (Equations (10) and (8)).
- RD – Rao diversity of the tree height at stand level (Equations (16) and (8)).

If trees with different traits or species are randomly distributed across the entire stand area (i.e., if they are not growing aggregated in patches and not regularly dispersed), each NDiv variable is closely related to its proportion-based counterpart. To demonstrate such relationships between SpeciesNDiv$_{stand}$ and SD and between HeightNDiv$_{stand}$ and RD, stands with random tree distributions were simulated. The tree locations of the 16 case-study plots were randomized in 1000 simulation runs and APA-maps were created and analyzed for each simulation. Trees in the core and buffer zones of the plots were only redistributed within their respective zone.

### 4. Results

The averaged values of the simulations showed the expected relationships between SD and SpeciesNDiv$_{stand}$ (Fig. 5A – Pearson correlation coefficient r = 0.997). The simulated SpeciesNDiv$_{stand}$-values were on average 0.012 points larger than the simulated SD-values (95 % confidence interval of [0.006, 0.018]). Similarly, the simulated average HeightNDiv$_{stand}$ and RD were strongly correlated (Fig. 6 A, r = 0.993) with average HeightNDiv$_{stand}$-values being 0.018 points larger than RD-values (95 % confidence interval of [0.015, 0.021]. The observed relationships of the real stands were considerably weaker (SpeciesNDiv$_{stand}$ and SD: r = 0.75; HeightNDiv$_{stand}$ and RD: r = 0.94). For the stands of this case-study, the spatial segregation of species seg(SpeciesNDiv$_{stand}$) was unrelated to SD (r = −0.07; Fig. 5B). Spatial segregation of the height seg(HeightNDiv$_{stand}$) was as well nearly unrelated to RD (r = 0.12; Fig. 6B).

**Table 1**

Characteristics of the 16 case-study plots of 0.25 ha size of mixed forests in Northern Germany. The mixture type is either European beech with Norway spruce or European beech with Douglas-fir. Columns to the right (starting with 'Beech proportion (APA)') are based on maps of the area potentially available (APA; Fig. 1 [plots 5.2 and 8.2] and Figure S1 in the supplementary material [all plots]). *'seg'* refers to the segregation index of the neighborhood diversity. The 'Beech proportion'-columns are calculated at species-level. All other columns refer to the stand-level.

| Plot label | Admixed species | Mean diameter at breast height (cm) | Mean height (m) | Stem density (ha$^{-1}$) | Basal area (m$^2$ ha$^{-1}$) | Beech proportion (basal area) | Beech proportion (APA) | $SpecNDiv_{stand}$ | $seg\text{-}SpecNDiv_{stand}$ | $HeightNDiv_{stand}$ | $seg\text{-}HeightNDiv_{stand}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1.2 | Douglas-fir | 47.6 (±23.0) | 34.6 (±9.4) | 236 | 51.62 | 0.17 | 0.32 | 0.31 | −4.00 | 0.34 | −3.66 |
| 1.4 | Spruce | 35.6 (±15.2) | 26.3 (±5.9) | 368 | 43.19 | 0.37 | 0.59 | 0.27 | −6.40 | 0.24 | −2.46 |
| 2.2 | D | 32.1 (±18.5) | 26.8 (±6.0) | 356 | 38.31 | 0.48 | 0.72 | 0.39 | −1.51 | 0.33 | 0.29 |
| 2.4 | S | 23.0 (±13.5) | 18.0 (±5.6) | 408 | 22.70 | 0.80 | 0.90 | 0.15 | −4.56 | 0.27 | −3.50 |
| 3.2 | D | 44.3 (±17.2) | 32.1 (±5.3) | 194 | 34.41 | 0.63 | 0.80 | 0.23 | −2.66 | 0.25 | −2.32 |
| 3.4 | S | 38.6 (±15.7) | 28.7 (±6.5) | 194 | 26.33 | 0.71 | 0.84 | 0.28 | −0.08 | 0.20 | −2.21 |
| 4.2 | D | 28.5 (±19.4) | 22.9 (±9.0) | 344 | 32.00 | 0.40 | 0.55 | 0.50 | −3.18 | 0.39 | −1.36 |
| 4.4 | S | 30.6 (±17.8) | 24.4 (±6.6) | 460 | 45.10 | 0.34 | 0.65 | 0.37 | −3.11 | 0.29 | −0.67 |
| 5.2 | D | 30.2 (±20.6) | 22.8 (±9.7) | 376 | 39.31 | 0.30 | 0.47 | 0.54 | 0.77 | 0.37 | −1.47 |
| 5.4 | S | 33.6 (±17.6) | 26.2 (±7.6) | 276 | 31.15 | 0.74 | 0.85 | 0.28 | 0.36 | 0.27 | −1.49 |
| 6.2 | D | 27.3 (±18.6) | 23.1 (±8.3) | 424 | 36.17 | 0.47 | 0.66 | 0.49 | −0.06 | 0.37 | −0.18 |
| 6.4 | S | 32.3 (±16.0) | 25.2 (±6.6) | 340 | 34.64 | 0.52 | 0.72 | 0.34 | −4.99 | 0.31 | 0.91 |
| 7.2 | D | 21.2 (±12.6) | 18.5 (±6.5) | 744 | 35.35 | 0.19 | 0.39 | 0.59 | −3.84 | 0.35 | −2.28 |
| 7.4 | S | 30.2 (±16.8) | 24.3 (±8.0) | 404 | 37.83 | 0.48 | 0.72 | 0.27 | −5.68 | 0.28 | −1.99 |
| 8.2 | D | 34.9 (±17.7) | 27.6 (±8.6) | 330 | 39.72 | 0.29 | 0.35 | 0.13 | −7.43 | 0.25 | −5.49 |
| 8.4 | S | 27.8 (±13.4) | 22.9 (±5.7) | 436 | 32.67 | 0.33 | 0.65 | 0.56 | 2.08 | 0.31 | 0.48 |
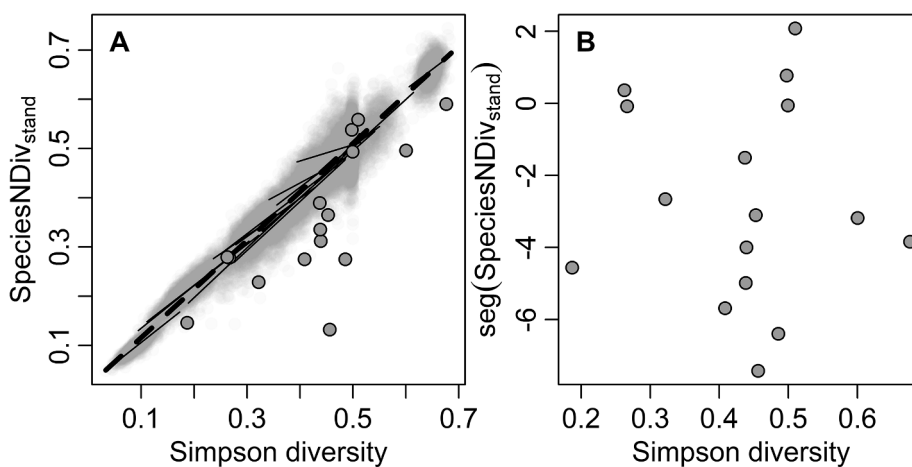


**Fig. 5.** Relationship between the species neighborhood diversity at stand-level (SpeciesNDivstand) and Simpson diversity (SD) (Panel A). Both variables are derived from APA-maps (Fig. 1). Transparent points represent 1000 simulations per plot of 16 case-study stands with randomized tree locations. Thin black lines show within-plot linear regression lines. The dashed black line is the linear regression line of the average values of the simulations per plot (SpeciesNDivstand = 0.02 + 0.99 SD; pearson correlation coefficient r = 0.997). Solid points are the value pairs of the real observations of SpeciesNDiv$_{stand}$ and SD (r = 0.75). Panel B shows the species segregation seg (SpeciesNDiv$_{stand}$) in relationship to SD (r = −0.07). Simpson diversity values larger than 0.5 are due to admixture of tree species other than beech, spruce or Douglas-fir.

According to seg(SpeciesNDiv$_{stand}$), in stand 5.2 tree species are distributed close to random (0.77) while stand 8.2 is the most extreme plot in terms of species aggregation (-7.43), which fits well to the visual impression of the maps (Fig. 1). The spatial separation of beech and Douglas-fir in plot 8.2 is the reason why its SpeciesNDiv$_{stand}$-value is so low (0.13). Even though Simpson diversity of plot 8.2 is high (0.46), direct interaction between beech and Douglas-fir is limited to only a small section of the plot at the boundary between the two large patches, which results in a low average neighborhood diversity.

## 5. Discussion

NDiv$_i$ is appropriate to assess relationships between biodiversity and processes at individual tree-level (e.g., growth, water uptake, mortality). Through upscaling, consistent descriptions of species and trait diversity at the stand- and species-level are provided.

When forest stands have random spatial tree distributions, the trait composition in the neighborhoods of individual trees is on average nearly identical to the trait composition of the overall stands.
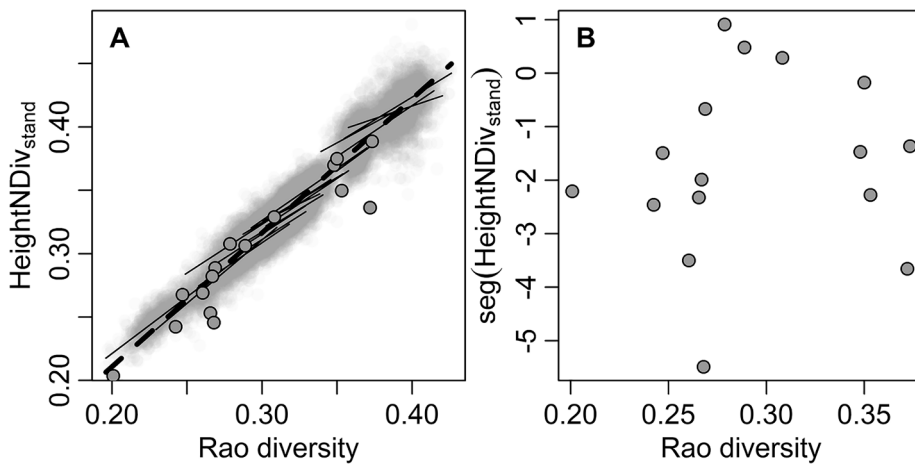
**Fig. 6.** Relationship between the height neighborhood diversity at stand-level (HeightNDiv$_{stand}$) and Rao diversity of the tree height (RD) (Panel A). Both variables are derived from APA-maps (Fig. 1). Transparent points represent 1000 simulations per plot of 16 case-study stands with randomized tree locations. Thin black lines show within-plot linear regression lines of the simulated values. The dashed black line is the linear regression line of the average values of the simulations per plot (HeightNDiv$_{stand}$ = −0.001 + 1.06 RD; Pearson correlation coefficient r = 0.993). Solid points are the value pairs of the real observations of HeightNDiv$_{stand}$ and RD (r = 0.94). Panel B shows the height segregation seg(HeightNDiv$_{stand}$) in relationship to RD (r = 0.12).

Consequently, the average simulated SpeciesNDiv$_{stand}$- and HeightNDiv$_{stand}$ -values from randomized spatial tree distributions of the case-study stands were nearly identical with values of Simpson and Rao diversity. This shows that NDiv-variables have a similar interpretation as some classic proportion-based diversity measures that are based on relative proportions only, if trees are randomly distributed across the stand area.

An aggregated spatial distribution of species and tree heights in some case-study stands resulted in observed SpeciesNDiv$_{stand}$- or HeightNDiv$_{stand}$-values that were substantially lower than Simpson or Rao diversity, depending on the degree of aggregation of trees of the same species or height. This indicates situations when use of NDiv$_{stand}$ may be most useful and in which cases use of conventional diversity measures is sufficient. Studies about forests that only consist of forest stands with random spatial tree configurations should not use NDiv$_{stand}$, as in this case conventional (proportion-based) diversity measures are simpler and equally informative. Use of NDiv$_{stand}$ (or any other measure of stand-level neighborhood diversity) would unnecessarily increase the complexity of an analysis. If stands have diverging spatial patterns, NDiv$_{stand}$ penalizes diversity of patch-wise in comparison to stem-wise mixed stands as they have a different potential for direct interaction between neighboring trees. In this case NDiv$_{stand}$ may be a useful way to account for the spatial configuration of a stand when describing relationships between biodiversity and ecosystem processes at stand-level, such as productivity or nutrient fluxes.

Many neighborhood diversity indices mainly use simple methods to define neighborhood structures and to calculate measures of neighborhood diversity that are based on neighbor distances. The advantage of nearest neighbor statistics is their simple implementation. If no tree coordinates are available, some nearest neighbor indices can be assessed directly in the field, which avoids time consuming measurement of distances and tree coordinates (Aguirre et al., 2003). As the size and shape of the APA-patch of a tree depend on the exact position and size of all competitors, APA-maps provide more detailed spatial information about tree neighborhoods, when tree coordinates are available. NDiv utilizes this additional spatial information from APA-maps to estimate neighborhood diversity. By considering tree size when upscaling from tree- to stand-level, NDiv$_{stand}$ may be more realistic than previous approaches, in particular in heterogeneous stands. The spatial distributions of the tree species of the case-study stands were probably caused by planting patterns during stand establishment when natural beech regeneration was artificially admixed with conifers. However, patch-wise mixing may occur in natural stands as well (Koukoulas and Blackburn, 2005; Janík et al., 2016). As there is a large variety of natural and human caused factors that may lead to different spatial configurations of forest stands, NDiv$_{stand}$ may be useful in many situations.

Besides interactions between neighboring trees, tree-level processes

may be influenced by indirect interactions that take place on larger spatial scales as well. For example, a considerable part of the litter fall of a tree may be dispersed by wind and influence soil properties in some distance from the tree (Nickmans et al., 2017). Through seed dispersal by animals or wind, trees may influence the composition of the understory over longer distances as well. In most of the cases tree processes are probably influenced by multiple mechanisms simultaneously that take place at different spatial scales. A holistic analysis of relationships between biodiversity and ecosystem processes needs to address the potential for interaction of trees at multiple spatial scales at the same time. However, as neighborhood-diversity and proportion-based diversity are correlated, it is difficult to clearly distinguish between their individual influences on stand-level processes using multivariate analysis techniques due to collinearity (Zuur et al., 2010). Use of the segregation-index seg(NDiv) together with the respective proportion-based counterpart of NDiv may avoid this issue as both are structurally independent. In the case-study stands both analyzed neighborhood variables (SpeciesNDiv$_{stand}$ and HeightNDiv$_{stand}$) were highly correlated to their proportion-based counterparts (Simpson and Rao diversity). The correlation between the segregation indices of both NDiv-variables and the respective proportion-based diversity index was rather low. The remaining correlation stems from slightly unbalanced sampling. Either Simpson- or Rao-diversity of the case-study stand could be used together with the segregation index of the respective NDiv-variable (seg(SpeciesNDiv$_{stand}$) or seg(HeightNDiv$_{stand}$)) as covariates in a regression analysis without issues due to collinearity. Relationships between the proportion-based stand composition at plot-level and segregation of tree traits or species (covariables) on an ecosystem process at stand-level (response variable) can be separated using this approach.

## CRediT authorship contribution statement

**Jonas Glatthorn:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Writing - original draft.

## 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108073.

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