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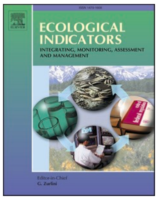

Original Articles

Towards a generalisation of the spatial species mingling diversity index

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ABSTRACT

Species diversity is an important notion of all ecosystems and much contributes to its inner functioning. Currently biodiversity is threatened by global changes including climate change. Spatial species mingling is a refinement of species diversity considering how individual plants of varying species are spatially mixed with those of others in local neighbourhoods. An important objective of conservation is to halt or at least to retard species diversity loss. A key element of monitoring systems, which can establish imminent threats to species, are reliable indices quantifying diversity. In this study, we proposed a generalised spatial species mingling index for an improved monitoring of how individual plants of certain species spatially mix with those of other species. A key feature of our new concept is a devaluation of instances of species inequality caused by recurrent neighbour species. The devaluation uses a memory function and is derived from proportional rules in multiwinner approval voting of political science. Our detailed analysis revealed that our new species mingling index has several statistical advantages over previous index concepts and is ecologically more plausible. Whilst dealing efficiently with recurrent species among the nearest neighbours, the new index is less dependent on global and local species richness than previous indices. Additionally, the index allows for adjustments by a parameter which can freely be chosen. Based on our analysis we recommend the use of our generalised species mingling index in the monitoring of spatial species diversity.

1. Introduction

Species diversity is one of the most important notions of many ecosystems worldwide. Many forest ecosystems in tropical and subtropical climate zones, for example, are very rich in tree species whilst tree species richness in boreal forests is often low. It is now well-established that high species diversity in ecosystems is not a 'luxury' property but fundamental to their existence (Yachi and Loreau, 1999; Begon et al., 2006; Matias et al., 2013; Oliver et al., 2015). For its importance species diversity has been considered one of the most important tenets of biodiversity (Kimmins, 2004). Currently biodiversity is threatened by multiple man-made global changes, among which climate change potentially has a particularly detrimental effect, since it proceeds at an unprecedented pace (McElwee, 2021; Román-Palacios and Wiens, 2020) so that not all species can adapt in time and survive. Worldwide conservation is therefore concerned with maintaining species diversity or at least with slowing down the process of losing species (Carvalheiro et al., 2013). Key to effective conservation is goal-oriented monitoring including the application of specialised summary statistics for measuring the current state of species diversity (Weiner and Solbrig, 1984; Pommerening and Grabarnik, 2019).

Spatial species mingling goes beyond the simple concept of species diversity and describes the spatial interactions of plant species, i.e. how individual plants of certain species are spatially mixed with those of other species (Pommerening et al., 2024a). To consider spatial species diversity in addition to non-spatial species diversity is a comparatively recent development supporting more precise diversity monitoring and conservation.

A simple approach to accounting for spatial species diversity is to consider the *mean number of heterospecific plants* or local species richness, i.e. species richness formed in structural groups including a given plant *i* (also termed reference or subject plant) and its *k* nearest neighbours:

$$M_i^* = \frac{s_i - 1}{k} \tag{1}$$

Here, s_i is local species richness, i.e. species richness among the k nearest neighbours of plant i including plant i itself. Species richness is defined

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as the absolute number of species without reference to area (Magurran, 2004). Eq. (1) is an example of a very basic and global approach where only species richness is considered almost non-spatially in a small cluster of plants around the subject plant. No distinction is made between subject plant and nearest neighbours, all plants are treated as one group. A weak spatial contribution to this index is only the fact that species richness is considered locally in the neighbourhood of each subject plant. Another limitation of Eq. (1) arises in situations where global species richness, i.e. the total number of species in a monitoring plot, $S < k + 1$. In that case, denominator k is strictly speaking not appropriate and should intuitively be replaced by S, since in that situation S is the maximum number of species that can exist in any neighbourhood group of $k+1$ plants.

Influenced by Pielou's (1977) segregation index, Gadow (1993) proposed spatial mingling index

$$M_i = \frac{1}{k}\sum_{j=1}^{k} \mathbf{1}\left(\mathrm{m}_i \neq \mathrm{m}_j\right), \tag{2}$$

which in contrast to Eq. (1) follows the principle of individual, pairwise comparisons, a method that is well-known from summary characteristics in point process statistics (Illian et al., 2008), and is applied to all other indices in the remainder of this paper. Point process statistics forms the theoretical basis of all indices discussed in this paper, since spatial neighbourhood indices can be interpreted as marks attached to the points of a point pattern (Pommerening and Grabarnik, 2019). According to this theory, spatial interactions between plants are specifically expressed by pairwise comparisons and any index value has to be interpreted from the point of view of subject plant i and in the light of pairwise comparisons.

More generally speaking, M_i is a *species inequality index* which is defined as the proportion of heterospecific pairs successively formed by a given plant i and its k nearest neighbours (Eq. (2)). The focus here is on how subject plant i mingles with its nearest neighbours. For Eq. (2) it is not important what species pattern the nearest neighbours form or what specific species are involved. Here, m_i denotes the species of subject plant i whilst m_j is the species of neighbour j. In Eq. (2), $\mathbf{1}(\mathrm{A})$ is an indicator function with $\mathbf{1}(\mathrm{A}) = 1$, if A is true, otherwise $\mathbf{1}(\mathrm{A}) = 0$. The indicator function in Eq. (2) essentially measures species inequality. In the analysis of mapped data, every plant within a given research plot acts once as reference plant i.

The species mingling index is expected to be more sensitive to spatial relationships and interactions than the mean number of heterospecific plants of Eq. (1). The central idea of this index is to quantify how plant species spatially mix and thus interact. This effort is similar to the way how in chemistry the spatial arrangement of atoms in a molecule is of interest. Although the emphasis still lies on the mingling of subject plant i, criticism has often been put forward with regard to extreme situations, where either all neighbours are of the same species (but different from that of the subject plant, Fig. 1A) or all $k+1$ plants are of different species (Fig. 1B). Both situations lead to exactly the same individual-plant index of $M_i = 1$. The performance of the mingling index is valid and correct in both situations, since M_i chiefly considers the spatial mixing of plant i which is considered in pairwise comparisons. However, when comparing the two situations in Fig. 1 it is difficult to ignore the notion that in the left case pairwise species inequalities are always caused by the same neighbour species (Fig. 1A) whilst in Fig. 1B four different species are involved in causing the same inequalities. One could therefore expect that these two situations should make an ecological difference to subject plant i, which also needs to be expressed numerically. In an attempt to improve on this perceived performance deficiency, Hui et al. (2008, 2011) proposed the *species-richness weighted mingling index*:

$$M_i^{'} = \frac{1}{k(k+1)}\sum_{j=1}^{k} \mathbf{1}\left(\mathrm{m}_i \neq \mathrm{m}_j\right) \times s_i \tag{3}$$

Accordingly, M_i of Eq. (2) is essentially multiplied by s_i, which is defined in the same way as for Eq. (1). With the species-richness weighted mingling index of Eq. (3) the *specificity* of neighbour species, i.e. which exact species occur in the neighbourhood of subject plant i, plays a much greater role than with the original mingling index of Eq. (2). Also with this index the same boundary problem as in Eq. (1) arises when global species richness $S < k + 1$. As a possible solution of this problem Wang et al. (2021) amended the original index definition by introducing term c to ensure that the maximum number of species that are theoretically possible in a group of $k+1$ plants is limited by the number of species present in the plant community stand or in the monitoring area studied:

$$M_i^{'} = \frac{1}{k \times c}\sum_{j=1}^{k} \mathbf{1}\left(\mathrm{m}_i \neq \mathrm{m}_j\right) \times s_i \text{ with } c = \min(S, k+1) \tag{4}$$

Cracknell et al. (2023) discovered that the species-richness weighted mingling index has been significantly positively correlated with the severity of ash dieback, a disease caused by the ascomycete fungus *Hymenoscyphus fraxineus* Baral, i.e. the infection was more severe in *F. excelsior* L. trees with fewer conspecific neighbours.

Though clearly an improvement from the point of view of those who criticised Eq. (2), cf. the values of M_i' in Fig. 1, the species-richness weighted mingling index of Eqs. (3) and (4) is also not fully satisfactory: It obviously mixes the concepts of mingling and local species richness, which makes interpretation more difficult. High species

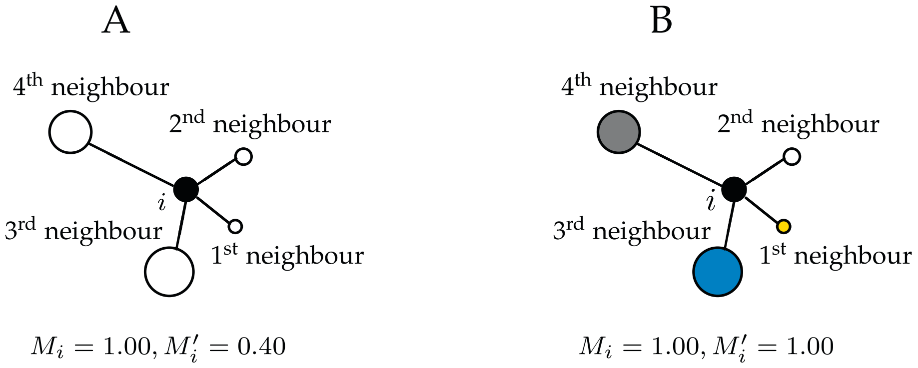

Fig. 1. Two extreme species mingling situations in a neighbourhood group involving $k = 4$ neighbours, where M_i (Eq. (2)) has the same value in both situations but M_i' (Eq. (3)) differs. A: In the first case, reference plant i is surrounded by four neighbours that are of a species different from that of the reference plant but all neighbour species are the same. B: In the second case, subject plant i is surrounded by four neighbours that are also of a species different from that of the subject plant and in addition all neighbour species are different from each other. Reference plants are indicated by index i and the colours used to fill the circular plant objects represent different species. The numbering of neighbours is not important for the index calculations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mingling can now be the result of high M_i and moderate local species richness or of moderate mingling and high s_i. The index also has the disadvantage of weighting M_i down considerably without options for adjustment; it also does not perform well in sampling. The species-richness weighted mingling index proves difficult to estimate from sample data: Local species richness s_i is prone to considerable localised variation in forests, which leads to high sampling errors in inventories (Pommerening et al., 2024b). In addition, the species-richness weighted mingling index mixes nearly non-spatial (Eq. (1)) and spatial (Eq. (2)) index concepts. There is also a strong, general dependence of all these mingling approaches on global species richness S. These are serious concerns for long-term diversity monitoring. All spatial species mingling indices reviewed in this section have bounds 0 and 1.

Problems similar to species mingling exist in general sciences beyond spatial species diversity. Chemistry and molecular structure have already been mentioned and other applications exist in materials science (Torquato, 2002). In general point process statistics, mingling is a problem of *mark inequality* where marks are (in this case qualitative) properties of points. In this statistical context, points are a general term for any location data of objects of interest such as plants and plant species can serve as qualitative marks (Illian et al., 2008).

The objective of this paper is to introduce a new mingling concept that avoids the aforementioned disadvantages whilst offering a meaningful and plausible solution in moderate and extreme species mingling situations when overall species diversity in neighbourhood groups is low. The intention of introducing the new concept is also to decrease the dependency of species mingling on global species richness and to avoid the need to quantify local species richness.

2. Materials and methods

2.1. An alternative and generalised species mingling index

Central to the new concept is a modification of the summables in Eq. (2) measuring species inequality. Instead of multiplying M_i with local species richness s_i as in Eqs. (3) and (4), the return value of the sum is modified, whenever the same neighbour species contribute to situations of $\mathrm{m}_i \neq \mathrm{m}_j$, i.e. species inequalities, more than once. The fundamental idea of this new, alternative species mingling approach has been inspired by proportional rules for multiwinner approval voting in political science where votes for already approved or elected political candidates are *devalued* in favour of votes for candidates or parties that so far have rarely received votes by applying so-called *divisor methods of apportionment* (Brams et al., 2019).

In analogy to proportional rules for multiwinner approval voting, pairwise situations of $\mathrm{m}_i \neq \mathrm{m}_j$ are devalued for subsequent plant neighbours, when this situation has already been caused by the same species m_j. This gives rare neighbour species causing $\mathrm{m}_i \neq \mathrm{m}_j$ a higher weight than more common neighbour species. Following Brams et al. (2019) such a devaluation can be achieved iteratively when considering pairs of plant and neighbours one after another by applying the following definition of a *generalised mingling index*:

$$M_i^{\mathrm{o}} = \frac{1}{k}\sum_{j=1}^{k}\frac{\mathbf{1}(m_i \neq m_j)\times h}{n(m_j)+h} \tag{5}$$

In Eq. (5), $n(m_j)$ is a memory function returning the number of times that the species of neighbour j has already occurred among the k nearest neighbours of subject plant i and at the same time contributed to cases of $m_i \neq m_j$. To a limited extent the memory function also takes the specificity of species in local neighbourhoods into account, however, much less so than local species richness s_i in Eqs. (3) and (4). With $j = 1$, $n(m_j) = 0$ for each newly considered subject plant i entering the calculation (cf. Fig. 2). As a consequence, $v_j = 1$ for the first instance of $m_i \neq m_j$, where $v_j = \frac{\mathbf{1}(m_i \neq m_j)\times h}{n(m_j)+h}$ in the same way as in Eq. (1).

Further contributions of $m_i \neq m_j$ by the same species m_j are now progressively devalued with each new instance of this species among the nearest neighbours (Fig. 2A). However, any contribution of $m_i \neq m_j$ by an unprecedented neighbour species receives again the highest and original value of 1 (Fig. 2B). Note that the plant neighbours do not need to be ordered in any particular way and M_i^{o} does not depend on the order in which neighbours and their species are considered. This is also true for the indices given in Eqs. (1)–(4). In contrast to Eqs. (3) and (4), no calculation of global or local species richness is required. In Eq. (5), h is a parameter that can freely be chosen. The larger parameter h the more gentle the devaluation is. For example, for $h = 1$, $n(m_j) = 0, \cdots, 3$ and $k = 4$, Eq. (5) produces $v_j = 1, \frac{1}{2}, \frac{1}{3}$ and $\frac{1}{4}$, whilst for $h = \frac{1}{2}$ we obtain $v_j = 1, \frac{1}{3}, \frac{1}{4}$ and $\frac{1}{5}$. Incidentally, for $h = 1$ Eq. (5) simplifies to

$$M_i^{\mathrm{o}} = \frac{1}{k}\sum_{j=1}^{k}\frac{\mathbf{1}(m_i \neq m_j)}{n(m_j)+1}. \tag{6}$$

Thus Eq. (6) is a special case of Eq. (5).

Applying different values of h in Eq. (5) provides an opportunity to adjust the new generalised mingling index according to the requirements of a given plant ecosystem. For example, when estimating mingling for species-rich woodlands (e.g. tropical rain forests), we hypothesise that h should be comparatively small whilst h should be 1 or > 1 in the analysis of woodland data with only few species, e.g. in European temperate or boreal forests. An appropriate choice of h can potentially counterbalance the influence of global species richness on the mingling index and make the index more focus on the spatial process of species mixing, which generally is of prime interest in the mingling

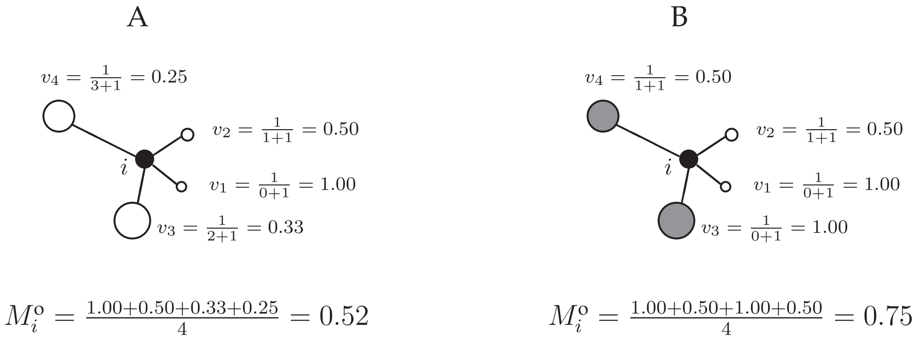

Fig. 2. Two hypothetical "structural groups of four" ($k = 4$) defining M_i^{o} according to Eq. (6)). Shadings indicate species, i.e. in the left case (A), all four neighbours are of the same species, which is different from that of the subject plant. In the right case (B), two of the four neighbours share the same species, which are both different from that of the subject plant. $v_1, \cdots, v_4$ are the four mingling scores resulting from pairwise comparisons and calculations. For comparison, species-richness weighted mingling index (Hui et al., 2008, 2011; Eq. (3)) is $M_i' = 0.40$ (left) and $M_i' = 0.60$ (right), respectively. The numbering of neighbours is not important for the index calculations.

concept. Therefore Eq. (5) and particularly devaluation-strength parameter h constitute a generalised way to define species mingling. Naturally h operates on a continuous scale, although obvious candidates borrowed from multiwinner approval voting are $h = 1$ (so-called Jefferson method) $h = \frac{1}{2}$ (so-called Webster method) and $h = \frac{2}{3}$ (Brams et al., 2019). The bounds of index M_i^o (Eq. (5)) are 0 and 1 and thus remain the same as those of the indices in Section 1. The index is not affected by any relabelling of species, using different numeric or text descriptors as long as the labelling of species is carried out consistently. In fact, the manner of species labelling does not matter, as the index essentially only considers whether the species of pairs of plants are the same or not, i.e. only species inequalities are taken into account.

2.2. *Data for testing the new mingling index concept*

We first analysed theoretical individual-plant index performance and then applied the different species mingling concepts of Eqs. (1)–(5) to six mapped data sets from varying forest ecosystems collected in different parts of the world. These six data sets were selected to follow an increasing trend of species richness and a decreasing trend of species evenness (Table 1). Also, they were deliberately chosen to originate from different parts of the world.

Manderscheid is a plot of mixed sessile oak (*Quercus petraea* Matt.) and European beech (*Fagus sylvatica* L.) in the Manderscheid Forest (50.11 N, 6.8 E) in Rhineland-Palatinate (Germany). Both species are in a mature stage and *F. sylvatica* occurs in small to medium-sized groups. Located in the Eifel mountains at 300–340 m asl the soil type is brown earth. This forest stand has been mainly managed for good quality oak timber, whilst beech timber was considered a minor by-product and the species' main purpose was to help improve the quality of oak timber (Pommerening, 2002; Pommerening and Uria-Diez, 2017).

The Walsdorf plot is part of a community forest in Rhineland-Palatinate (Germany). Also located in the Eifel mountains (50.17 N, 6.42 E) at 560–580 m asl the soil type is a fresh brown earth. The stand is dominated by European beech (*Fagus sylvatica* L.) mixed with Norway spruce (*Picea abies* (L.) Karst.) occurring in small groups and a minor contribution of individual sessile oak (*Quercus petraea* Matt.) (Gadow et al., 2012).

The Białowieża data are from Białowieża Forest (50.43 N, 23.50 E) in eastern Poland in the border zone between Poland and Belorussia. The woodland consists of a pedunculate oak (*Quercus robur* L.) overstorey interspersed with Scots pine (*Pinus sylvestris* L.) and an understorey of Norway spruce (Picea abies (L.) Karst.), hornbeam (*Carpinus betulus* L.) and silver birch (*Betula pendula* Roth.). The data are from outside the strict reserve of Białowieża Forest and the forest stand is managed for biodiversity and timber value according to the principles of low-impact continuous cover forestry (Pommerening and Stoyan, 2008; Pommerening and Uria-Diez, 2017).

The Hidegvizvölgy woodland is located in the buffer zone of the Hidegvizvölgy Forest Reserve (47.34 N, 17.37 E) in the hills around the northwest Hungarian city of Sopron. Before being designated as a forest reserve in the early 2000s, the area was part of the restricted border zone of the Iron Curtain for almost 50 years and consequently remained undisturbed for a comparatively long time (Puttkamer, 2005; Pommerening and Uria-Diez, 2017). The main species of this forest stand include sessile oak (*Quercus petraea* Matt.), hornbeam (*Carpinus betulus* L.) and European beech (*Fagus sylvatica* L.).

Clocaenog Forest lies on the southern side of the Denbigh moors (Wales, UK), a plateau rising to between 300 m and 500 m asl. The forest stand (Tyfiant Coed plot 6 at 53.04N, 3.27 W) included in this study is situated at an altitude of 350 m asl. Podzolic brown earth predominates on this site. The climate is relatively harsh with cool temperatures and high rainfall. Rainfall is in excess of 1300 mm. The site was originally planted with Japanese larch (*Larix kaempferi* (Lamb.) Carr.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in 1932. Sitka and Norway spruce (*Picea sitchensis* (Bong.) Carr. and *Picea abies* L. Karst., respectively) colonised the forest area from adjacent stands in the late 1990 s (Pommerening et al., 2024b).

Xiaolongshan Forest is located in the Xiaolongshan Nature Reserve, Gansu province, north-west China. The forest is situated on the north-facing slopes of the West Qinling Mountain range (33.30–34.49 N, 104.22–106.43 E) and constitutes a natural mixed pine-oak forest. The soil type is a grey cinnamon soil in the north of the Qinling Mountains and yellow cinnamon soil prevails in the south. Plot b from the Xiaolongshan Forest was included in this study. This stand is a mixed pine-oak population dominated by *Quercus aliena* var. *acuteserrata* Maxim., *Ulmus glabra* Huds. and *Symplocos paniculata* (Thunb.) Wall. ex D. Don. (Pommerening et al., 2019; Wang et al., 2021).

The largest number of trees per hectare can be found at Xialongshan in China closely followed by Hungarian Hidegvizvölgy (Table 1). The lowest number of trees, approximately 30 % of those at Xialongshan, was observed at Clocaenog in Wales. Basal area, an expression of size-dependent tree density, is highest at Hidegvizvölgy and has a minimum of 57 % of the maximum at Xialongshan. Together with the arithmetic mean stem diameter these data tell us that Xialongshan represents a fairly early development stage while Manderscheid, Walsdorf and Clocaenog are more mature. At Białowieża, Clocaenog and Xialongshan maximum stem diameters lie between 70 and 80 cm (Table 1).

The aggregation index by Clark and Evans (1954), R', adds spatial information on inhomogeneity and clustering of tree locations. While the location patterns at Manderscheid and Clocaenog suggest approximate spatial randomness with R' close to 1, the tree locations at Walsdorf markedly tend towards regularity ($R' > 1$), which is probably a legacy of former plantation management in this case. On the other hand there are instances of moderate clustering ($R' < 1$) at Białowieża, Hidegvizvölgy and Xialongshan, representing forest stands that were either completely

Table 1
Main characteristics of the six experimental woodland data sets: Area in hectare, A, global species richness, i.e. the absolute number of species, S, species evenness, E, calculated as $E = D/S$ based on Simpson index (1949) with D defined as $D = 1 - \sum_{i=1}^{S} p_i^2$, where p_i is the proportion of individuals found in the ith species, Clark and Evans (1954) aggregation index, R', number of trees per hectare, N, basal area in m^2 per hectare, G, mean stem diameter in cm, $\overline{d}$, minimum stem diameter in cm, $d_{\min}$, maximum stem diameter in cm, $d_{\max}$. The Clark and Evans (1954) aggregation index, R', was calculated using the NN1 spatial edge correction method (Pommerening and Stoyan, 2006).

Characteristic	Manderscheid	Walsdorf	Białowieża	Hidegvizvölgy	Clocaenog	Xialongshan
A	0.64	1.26	1.02	0.67	1.05	0.49
S	2	3	5	7	11	35
E	0.222	0.147	0.115	0.106	0.067	0.026
R'	1.03	1.23	0.89	0.93	1.04	0.88
N	381	503	749	782	257	842
G	28.7	35.0	34.9	44.3	29.0	25.3
$\overline{d}$	28.3	27.8	18.5	24.4	30.6	16.5
$d_{\min}$	11.2	7.1	5.0	6.2	5.1	4.4
$d_{\max}$	60.5	58.9	79.1	57.2	77.2	70.5

unmanaged or managed in an ecologically sensitive way (Table 1).

3. Results

3.1. Index performance under boundary conditions

In the context of spatial species diversity, boundary conditions theoretically exist when overall species richness S is either very low or very high. In connection with the mingling indices defined in Eqs. (1) and (3), the problem of $S < k+1$ was already alluded to in the introduction of this paper: In local neighbourhoods including k neighbours there can only be a maximum of S heterospecific species provided $S < k+1$. When $S \geq k+1$, there is no boundary problem, since there is a sufficient number of species available in the population so that subject plant i and the k nearest neighbours can all be of different species. For the species mingling index to yield ecologically meaningful results, at least two species are required to exist in the population, i.e. $S = 2$. Assuming $k = 4$ neighbours, as is often applied in the literature, a boundary problem exists in this situation as would be for all $S < k+1$. In the case of $k = 4$, any $S = 2, \cdots, 4$ satisfy this condition. The most critical situation, however, exists for $S = 2$ (Fig. 3).

The theoretical analysis in Fig. 3 revealed that simple, non-spatial mingling index M_i^* (Eq. (1)) produces only two index values throughout the $k+1$ mingling scenarios, i.e. 0 and 0.25, which nicely illustrates the difference between local species richness and spatial species mingling. Obviously this simple index is not very sensitive to different configurations of subject tree and nearest neighbours. Traditional mingling index M_i (Eq. (2)) clearly distinguishes the $k+1$ mingling scenarios, however, particularly the result obtained for scenario $k+1$ (Fig. 3E), where all neighbours are of the same species, which is different from that of subject plant i, has often been criticised for its high score of 1 despite an obvious lack of species diversity among the k nearest neighbours as previously noted.

Starting with the scenario of only one heterospecific neighbour, species-richness weighted mingling index M_i' (Eq. (3)) reduces M_i considerably starting with a value of 0.10 (Fig. 3B) and finally arriving at 0.40 (Fig. 3E). Incidentally, amended Eq. (4) would under these boundary conditions of $S = 2$ produce the same results as Eq. (2).

With new alternative mingling index M_i^{o} (Eq. (5)) the index values are exactly the same as for M_i, when the first two mingling scenarios are considered (Fig. 3A and B), i.e. none or one of the nearest neighbours are of the other species. Unlike in the case of M_i' (Eq. (3)), the devaluation is not activated in the second scenario (Fig. 3B) because there is only one heterospecific neighbour causing $m_i \neq m_j$ by this species. For the following scenarios in Fig. 3C–E we can see an increasing sequence of values (when considering the same value of h). When modifying h it is clear that resulting M_i^{o} only vary little for comparatively low values of M_i, but the differences caused by h increase with increasing M_i. Though M_i^{o} appears to approach M_i' for $h \approx \frac{1}{4}$, it is not possible to find a value of h analytically so that the results of both indices would match.

Another valid question relating to boundary conditions is how increasing numbers of nearest neighbours affect the mingling indices. For example, we can return to Fig. 3E where subject plant i is of one species and all four neighbours are of the same species which is different from that of species i. We can now imagine that we iteratively add

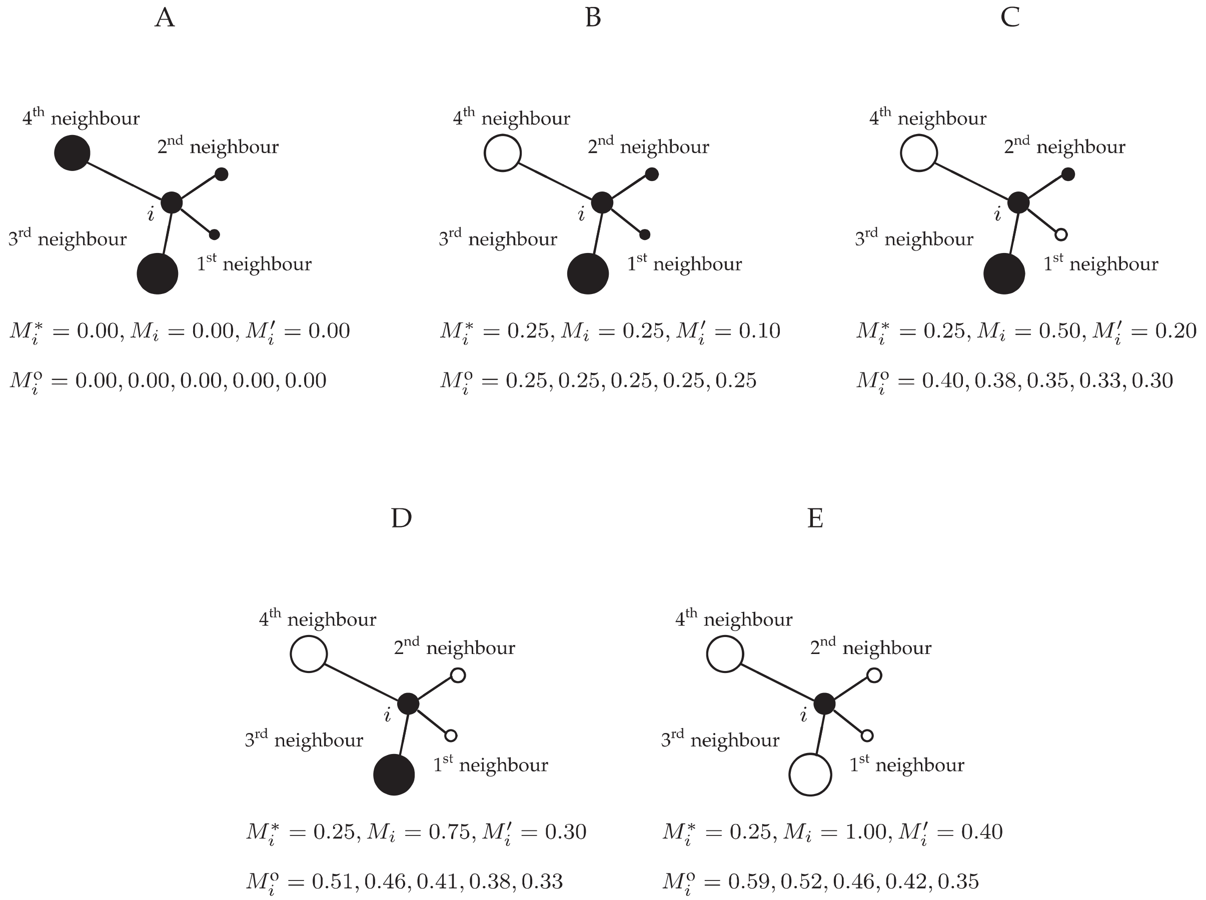

Fig. 3. Hypothetical "structural groups of four" ($k = 4$) including two species indicated by filled (black) and unfilled (white) circular objects. For completeness and better orientation, the neighbours are numbered according to increasing distance from reference plant i, but this ordering is not important for any of the mingling indices of this paper. The numbers below each structural group give the results of Eqs. (1)–(3) and (5). For the generalised, alternative mingling index M_i^{o} (Eq. (5)) different values of h were applied, i.e. $h = 1\frac{1}{2}, 1, \frac{2}{3}, \frac{1}{2}, \frac{1}{4}$ (second row).

nearest neighbours and while doing so any new nearest neighbour adopts the same species as the already existing nearest neighbours. Index $M_i = 1.00$ would remain the same with increasing k, but $M_i^*, M_i^{'}$ and M_i° keep decreasing to gradually display asymptotic behaviour (Fig. 4).

M_i° steadily decreases from $M_i^{\circ} = 1$ to a devaluated quantity < 1 that depends on h. As expected, the smaller h the lower the final asymptote formed by the corresponding devaluation curve. The five curves produce a layered system without intersections. Therefore when all else is kept constant, increasing numbers of k lead to an increasing devaluation of M_i, which from both an ecological and a statistical point of view is a plausible outcome.

For, $M_i^{'}$, however, as per definition, there is only one resulting curve given the same experiment as previously described. This curve is located between the M_i° curves for $h = 0.25$ and $h = 0.50$ indicating that in this two-species case, $M_i^{'}$ is close to M_i° with rather low h. In a way the use of different h helps approximate the strength of devaluation caused by $M_i^{'}$ and the location of the continuous grey curve confirms that the devaluation achieved by $M_i^{'}$ is indeed rather strong. For $k = 1, M_i^{'} = 1.0$ in this case of $S = 2$. Also the definition of M_i^* produces a devaluation curve, which is located considerably lower than all other curves in Fig. 4. While the definitions of indices M_i^* and $M_i^{'}$ offer no choices and only result in a single curve each in Fig. 4, new index M_i° gives analysts some opportunities to choose from by varying parameter h.

3.2. Performance with $S = 5$

In another theoretical example involving $S = 5$ and $k = 4$, we can clearly see how both competing mingling indices, $M_i^{'}$ and M_i°, steadily increase with increasing spatial species complexity in neighbourhood groups (Fig. 5). However, index $M_i^{'}$ cannot differentiate between situations h) and i) in Fig. 5, i.e. a situation where species 3 occurs only once and another one where species 3 occurs twice, whilst index M_i° clearly shows this expected difference. In situation h) a whole devaluation sequence involving $v_j = 1, 0.5, 1, 0.33$ over three neighbours of the same species takes place, whilst in situation i) two separate and shorter v_j devaluation events are triggered with an overall effect which is smaller compared to a sequence, i.e. $v_j = 1, 0.5, 1, 0.5$.

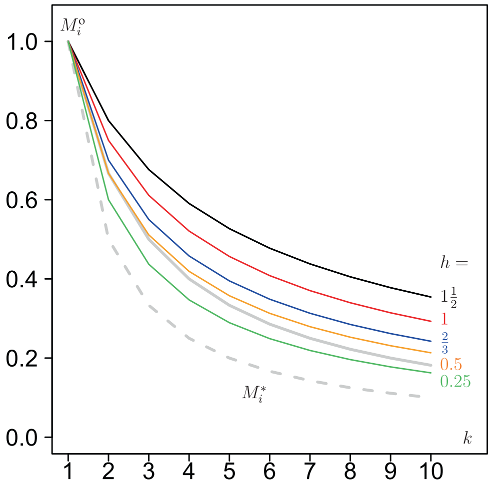

Fig. 4. Mingling indices M_i^* (Eq. (1)), $M_i^{'}$ (Eq. (3)) and M_i° (Eq. (5)) with different values of h. The number of nearest neighbours k varied between 1 and 10. Subject plant i always was of a species different from the species of the k neighbours, but all neighbours shared the same species, i.e. an underlying bivariate pattern with species richness $S = 2$ was assumed. The continuous grey line represents index $M_i^{'}$, while the dashed grey line is associated with index M_i^*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

On the other hand, situations i) and j) in Fig. 5 are judged by both competitive indices to result in the same degree of spatial species diversity: A situation with only two species among the nearest neighbours which occur twice each (leading again to two separate short devaluations of v_j) and a situation with four species among the nearest neighbour of which one matches that of subject plant i, however, without any devaluation of $v_j = 1$. Assigning the same degree of spatial diversity to both situations seems a plausible outcome, since $v_j = 1, 0, 1, 1$ for the subject plant in situation j) and the sum of v_j is exactly the same as the v_j sum for the subject plant in Fig. 5i). Both mingling indices considerably increased from spatial species situation j) to k), because in Fig. 5k) all four neighbours have species that are different from that of the subject plant whilst in Fig. 5j) one neighbour species matches that of the subject plant. However, one devaluation takes place in Fig. 5k), which only leads to a minor reduction of M_i°.

As an outcome of the analysis of Fig. 5 we can conclude: In terms of overall impact, neighbour species matching the species of the subject plant have the greatest devaluation effect and reduce the value of M_i° most. This is followed by situations where the result of $m_i \neq m_j$ is devalued by h. Devaluations by h reduce M_i° more, if occurring in a sequence over more than two neighbours of the same species. Devaluations over only two neighbours have the smallest effect. This conclusion directly follows from the definition of M_i° in Eq. (5).

3.3. Relationship between competing species mingling indices

When depicting the values of the closest index competitors M_i° over $M_i^{'}$ in scatterplots, semi-discrete arrangements of data pairs result whose trends can be highlighted by curves (Fig. 6). The deviation of these trend curves from the 1: 1 line follows a parabolic shape arching above the 1: 1 line. For $S \geq k+1$ the largest deviation from the 1: 1 line is approximately in the vertex of the parabola curve, i.e. in the medium range of $M_i^{'}$, whilst both indices have the same values at $M_i^{'} = 0$. This implies that for $S \geq k+1$ M_i° dampens the reducing effect of $M_i^{'}$ most near the vertex, i.e. the devaluation of species mingling is reduced by a maximum at this point. The fact that $M_i^{\circ} > M_i^{'}$ in nearly all cases clearly shows that M_i° puts more emphasis on the process of species mingling than $M_i^{'}$.

With increasing global species richness S, the maximum values of both indices coincide at 1. In Fig. 6, this is the case for Clocaenog and Xialongshan (Fig. 6, bottom centre and right). Incidentally, values of $M_i^{'} = 1$ and $M_i^{\circ} = 1$ only happen for one tree at Clocaenog and for 41 trees at Xialongshan, i.e. these are clearly rare events. As previously explained, h does not apply in these cases.

The other interesting observation is that the trend curves form a layered system with the curve representing $h = 1.5$ being always on top and the curve produced by $h = 0.5$ always at the bottom (Fig. 6). This corresponds to the known fact that larger values of h lead to more gentle devaluations than smaller ones and this trend directly follows from Eq. (5). Interestingly, the sum of squared residuals obtained from fitting the trend curves increases with decreasing values of h. This implies that decreasing values of h not only devalue M_i more but also do this in a more variable way which makes statistical fitting more difficult, but may ecologically be more interesting and realistic. This increasing variability for decreasing h potentially makes the two index concepts compared here more independent from each other.

The distances between the four curves near the vertex and near $M_i^{'} = 1$ diminish with larger S. This is caused by the $M_i^{\circ} \sim M_i^{'}$ scatterplot data, which are more compact for larger S. As a consequence, for small S the choice of h is of greater significance than in ecosystems with large S. Global species richness S has apparently a strong influence on the relationship $M_i^{\circ} \sim M_i^{'}$. For $k = 4$, only with larger values of S, e.g. $S = 11$, values of $M_i^{'} = 1$ and $M_i^{\circ} = 1$ are achieved (Fig. 6).

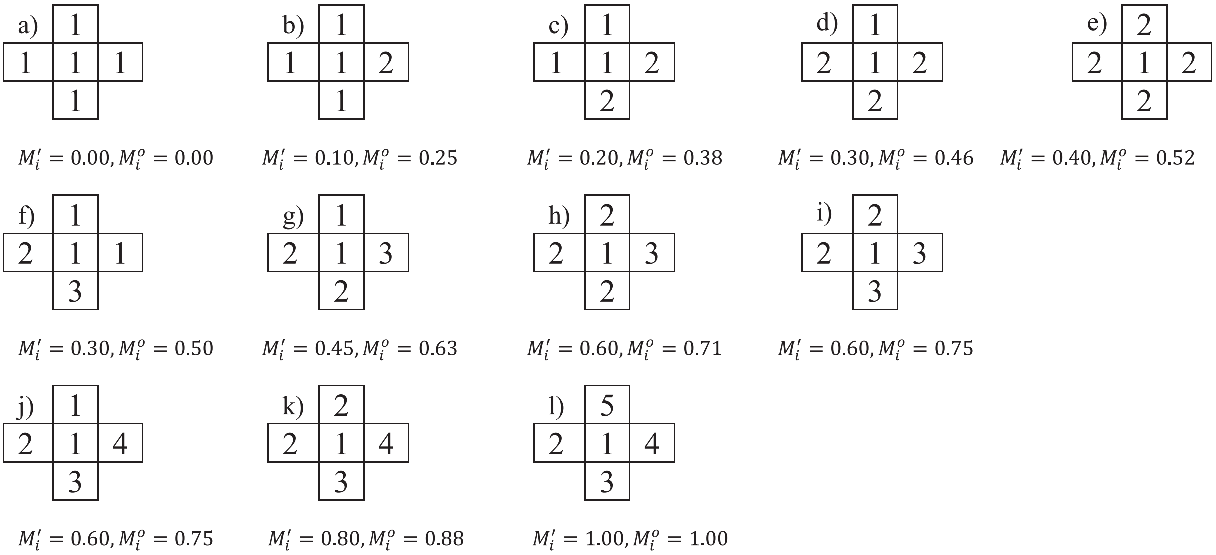

Fig. 5. Schematic worked example involving 12 selected subject plants and their $k = 4$ neighbours. Subject plants i are located in the centre of the schematic cross structures and cells extending from the centres represent nearest neighbours. Species are indicated by numbers 1–5 and global species richness is assumed as $S = 5$. Mingling indices M_i' (Eq. (3)) and M_i^o (Eq. (5)) with $h = 1$ are given.

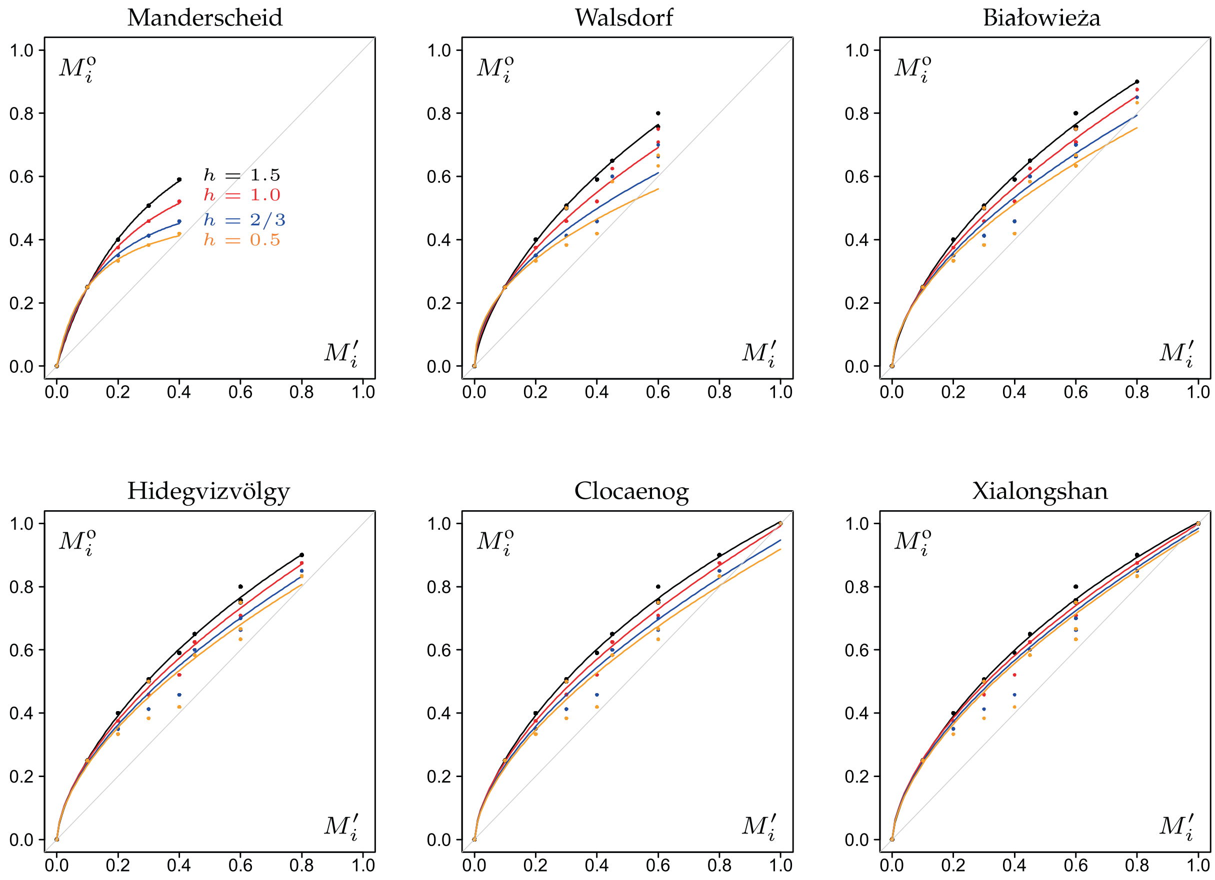

Fig. 6. Scatterplots of M_i' (Eq. (3)) and M_i^o (Eq. (5)) with different values of h given in the top left scatterplot. The number of nearest neighbours is $k = 4$. The trend curves follow a variant of the model by Chapman-Richards (Pienaar and Turnbull, 1973), i.e. $M_i^o = a \times \left(1 - e^{-b \times M_i'}\right)^c$. We used only data points not affected by edge effects, i.e. where the distance between subject tree and 4th nearest neighbour was shorter than the distance between subject tree and the nearest point of the observation window, i.e. the boundary polygon of the mapped data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Population species mingling indices

Mean population species mingling calculated as an arithmetic mean of individual-tree species mingling indices and applying the NN1 edge correction (Pommerening and Stoyan, 2006) tends to increase with increasing global species richness S and with decreasing species evenness E (Table 1, Table 2). This can clearly be seen from all five index variants. Some woodlands, e.g. Walsdorf and Clocaenog, have smaller $\overline{M}$ values than one would expect from their S values, an effect, which most likely is related to the degree of clustering (Table 1). For example, Walsdorf and Clocaenog show a markedly larger value of R', i.e. more regularity, than Manderscheid and Hidegvizvölgy, whereas clusters and their boundary zones are suspected to offer more opportunities for high mingling.

As expected, the highest mingling values are those of the original 1993 index, $\overline{M}$ (Eq. (2)). Species-richness weighted mingling index $\overline{M}'$ (Eq. (3)), always shows mean values and 95 % confidence intervals not far removed from those of simple index $\overline{M}^*$ (Eq. (1)), which is based on local species richness only. This intriguing similarity of the means of Eqs. (1) and (3) emphasises how much the species-richness weighted mingling index is influenced by local species richness.

As expected, both variants of the species-richness weighted mingling index, i.e. Eqs. (3) and (4), always lead to the same population means provided $S \geq k+1$ (Table 2). For Manderscheid and Walsdorf this condition is not satisfied and therefore the two index variants vary here. Whilst at Manderscheid with $S = 2$ Eq. (4) yields exactly the same mean as the original species mingling index of Eq. (2), at Walsdorf with $S = 3$ $\overline{M}'$ (Eq. (4)) gives a value between $\overline{M}'$ (Eq. (3)) and $\overline{M}$ (Eq. (2)).

$\overline{M}^{\circ}$ (Eq. (5)) values with $h = 1.5$ are roughly less by 0.10 than $\overline{M}$ and therefore considerably larger than $\overline{M}'$ (Eq. (3)). The continued devaluation caused by decreasing h is very gradual and even the difference in $\overline{M}^{\circ}$ for $h = 1.5$ and $h = 0.5$ is no more than 0.05 (Table 2). Overall the fact that $\overline{M}^{\circ} > \overline{M}'$ in all cases and that the corresponding 95 % confidence intervals do not overlap (except for Walsdorf with $h = 1.5$) prove once more that $\overline{M}^{\circ}$ puts more emphasis on the process of mingling than $\overline{M}'$.

3.5. Proportions of trees affected by mingling devaluation

It is also instructive to analyse the proportions of trees affected by mingling devaluations caused by M_i° (Eq. (5)) and M_i' (Eq. (3)). For this purpose we defined a deviation measure $M_i - M_i^{\circ}$ and $M_i - M_i'$, which for simplicity we collectively referred to as D in both cases. Deviation measure D typically yields a comparatively small number of discrete values for which tree proportions can be calculated. The sum of proportions of trees where mingling is affected by devaluation is always much lower when applying M_i° as compared to M_i'. On average, only 47 % of all tree M_i values are affected by M_i° while on average M_i' affects M_i of 80 % of trees (Fig. 7).

The detailed breakdown of proportions provided by the curves in Fig. 7 highlight the fact that the mingling of nearly 50 % of trees is unaffected by M_i° in all woodland plots with the exception of Walsdorf. Here the percentage is much higher and nearly 80 %, probably due to a common lack of situations with $v_j = 1$. For $D > 0$ many red curves relating to M_i' lie above the blue ones which are associated with M_i° (Fig. 7). The M_i' curves also extend to larger values of D, owing to the fact that M_i' often leads to a greater devaluation than M_i° particularly in the central mingling range. With the M_i° curves the decrease in proportions largely follows the sequence of D values, whilst for M_i' often maximum D is not at 0 but at some other value $D > 0.1$.

4. Discussion

Species diversity including spatial species diversity currently is a hot topic in the international biodiversity community and is likely to continue to be so. Given the seriousness of this field and its complexity in the context of current global developments, there cannot even be enough alternative approaches to quantifying species diversity including spatial species diversity in the literature so that one may choose carefully. A diverse range of different methods offers the opportunity to test candidate diversity indices and to select the most suitable of them given a specific ecosystem or research question.

In this study, we proposed a new index M_i° (Eq. (5)) for the improved monitoring of spatial species mingling, which generally speaking focusses on how individual plants of certain species are spatially mixed with those of other species. A key feature of the new concept is a devaluation of the results of pairwise comparisons of subject plant and nearest neighbour where both plants are of different species. Devaluation of maximum score $v_j = 1$ assigned to such comparative situations takes place when this inequality has previously been caused by the same neighbour species. This strategy of improving the spatial species mingling index is consistent with the observation that common species contribute little to spatial patterns of functional diversity (White et al.,

Table 2
Species mingling population means along with the corresponding 95 % confidence intervals calculated for the six example woodland data using the NN1 spatial edge correction method (Pommerening and Stoyan, 2006). The confidence intervals were estimated using R package `bootstrap` and function `boot()`.

Characteristic	Manderscheid	Walsdorf	Białowieża
$\overline{M}^*$ (Eq. (1))	0.2103 (0.193, 0.222)	0.1379 (0.136, 0.159)	0.2750 (0.259, 0.285)
$\overline{M}$(Eq. (2))	**0.4280 (0.367, 0.464)**	**0.2310 (0.221, 0.269)**	**0.4646 (0.432, 0.481)**
$\overline{M}'$(Eq. (3))	0.1712 (0.149, 0.185)	0.0966 (0.092, 0.115)	0.2288 (0.211, 0.241)
$\overline{M}'$(Eq. (4))	0.4280 (0.378, 0.455)	0.1609 (0.154, 0.187)	0.2288 (0.210, 0.237)
$\overline{M}^{\circ}$(Eq. (5)), $h = 1.5$)	0.3234 (0.291, 0.348)	0.1872 (0.181, 0.215)	0.3769 (0.354, 0.392)
$\overline{M}^{\circ}$(Eq. (5)), $h = 1.0$)	0.3023 (0.278, 0.319)	0.1782 (0.172, 0.210)	0.3584 (0.338, 0.372)
$\overline{M}^{\circ}$(Eq. (5)), $h = 2/3$)	0.2823 (0.255, 0.293)	0.1696 (0.164, 0.196)	0.3407 (0.319, 0.355)
$\overline{M}^{\circ}$(Eq. (5)), $h = 0.5$)	0.2696 (0.243, 0.288)	0.1640 (0.160, 0.189)	0.3292 (0.309, 0.341)
Characteristic	**Hidegvizvölgy**	**Clocaenog**	**Xialongshan**
$\overline{M}^*$ (Eq. (1))	0.3875 (0.375, 0.410)	0.3497 (0.332, 0.376)	0.6332 (0.614, 0.660)
$\overline{M}$(Eq. (2))	**0.5912 (0.560, 0.621)**	**0.5613 (0.538, 0.630)**	**0.7778 (0.743, 0.801)**
$\overline{M}'$(Eq. (3))	0.3376 (0.326, 0.366)	0.3069 (0.286, 0.342)	0.5845 (0.560, 0.610)
$\overline{M}'$(Eq. (4))	0.3376 (0.321, 0.367)	0.3069 (0.284, 0.342)	0.5845 (0.557, 0.615)
$\overline{M}^{\circ}$(Eq. (5)), $h = 1.5$)	0.4993 (0.477, 0.527)	0.4640 (0.448, 0.511)	0.7154 (0.692, 0.734)
$\overline{M}^{\circ}$(Eq. (5)), $h = 1.0$)	0.4794 (0.462, 0.503)	0.4433 (0.428, 0.479)	0.7011 (0.676. 0.722)
$\overline{M}^{\circ}$(Eq. (5)), $h = 2/3$)	0.4601 (0.442, 0.482)	0.4234 (0.403, 0.473)	0.6871 (0.662, 0.711)
$\overline{M}^{\circ}$(Eq. (5)), $h = 0.5$)	0.4475 (0.427, 0.468)	0.4106 (0.390, 0.447)	0.6779 (0.658, 0.700)

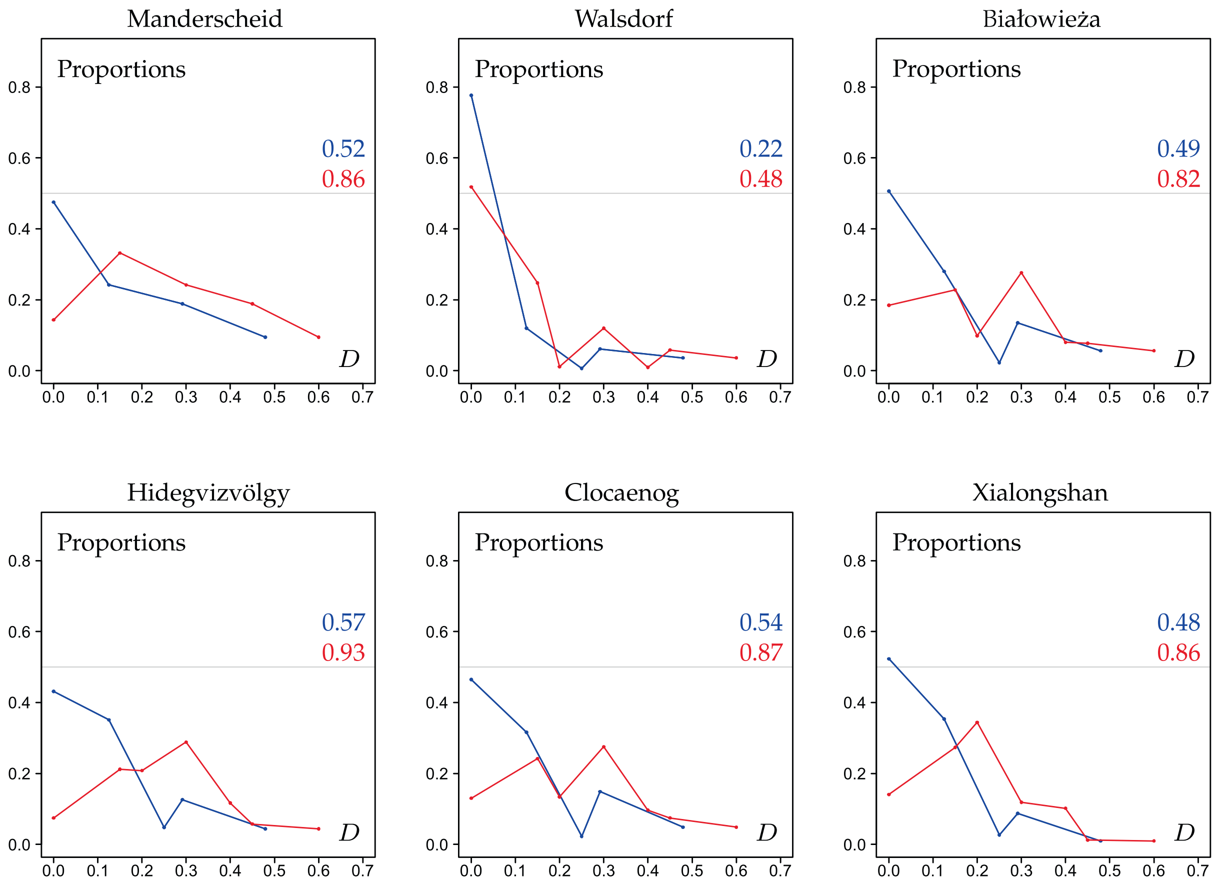

Fig. 7. Proportions of M_i (Eq. (2)) of trees affected by M_i^{o} with $h = 1.0$ (Eq. (5)), blue) and M_i' (Eq. (3)), red). The effects were calculated as $M_i - M_i^{\text{o}}$ and $M_i - M_i'$, which for simplicity are collectively referred to as deviation D. The horizontal line denotes the proportion of 0.5 and the numbers above this horizontal line give the cumulative proportions of M_i devalued by M_i^{o} and M_i', i.e. for $D > 0$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2022).

As our analysis has revealed, the new alternative species mingling index has several advantages over a previous modification by Hui et al. (2008, 2011), M_i' (Eq. (3)): The new concept is less dependent on global and local species richness. This also includes situations where global species richness is smaller than the number of nearest neighbours plus the subject tree. Such situations constitute boundary conditions which are not easy to handle. The new species mingling index M_i^{o} avoids this problem altogether. The new alternative index also has the advantage that the strength of devaluation can be freely chosen by defining devaluation-strength parameter h. This option offers the opportunity to customise the dependence of the index on global species richness so that the focus remains to be on species mingling. To achieve this it could be a plausible strategy to select small values of h for applications in species-rich ecosystems and comparatively large h in ecosystems where only few species occur. Future research needs to establish whether and how h should be selected in dependence on global species richness. The new index could also be instrumental in ascertaining whether low local species richness or low spatial mingling or both were responsible for the strong correlation of the species-richness weighted mingling index with the severity of ash dieback in Cracknell et al. (2023).

Mingling devaluation curves resulting from the application of different values of h in Eq. (5) always form a layered system with curves representing $h = 1.5$ being always on top of the system and curves resulting from $h = 0.5$ are always at the bottom.

The new alternative species mingling index M_i^{o} also shows a plausible behaviour in situations where the spatial plant pattern remains unchanged but the number of nearest neighbours k increases when recomputing the index. In that case, devaluation steadily increases with increasing k leading to an asymptotic behaviour, which is satisfactory and ecologically plausible. The location of the devaluation curves again depends on parameter h (Fig. 4). We also found evidence for the fact that M_i^{o} can recognise more different spatial neighbourhood situations than M_i' (Fig. 5).

Even for small h index M_i^{o} typically devalues species mingling less than index M_i', particularly in the central range of the mingling values (Fig. 6). The observation that $M_i^{\text{o}} > M_i'$ in nearly all cases clearly highlights that M_i^{o} puts more emphasis on species mingling and less on species richness, which is what was intended with the introduction of this new concept. On average across all six woodland datasets the mingling values of only 47 % of all trees were modified by M_i^{o} while M_i' affected the mingling of 80 % of trees. This shows that M_i^{o} constitutes an approach that modifies the original mingling concept of M_i (Eq. (2)) much less than M_i' whilst still achieving an efficient devaluation and modification of the aummables inside the sum of Eq. (5) in situations where the same neighbour species recur.

The results of calculating population means of the different mingling indices for the six woodland data highlighted once more that index M_i' is mostly influenced by local species richness and less by actual mingling. The results also showed that the influence of h on the population means is comparatively small. Also the analysis of population means revealed that index M_i^{o} puts more emphasis on species mingling than index M_i'.

5. Conclusions

Our comprehensive sensitivity analyses revealed that the new species mingling index M_i^o (Eq. (5)) clearly has a great potential for quantifying spatial species mingling in diverse and not so diverse plant ecosystems alike. M_i^o is a generalisation of previous mingling approaches and avoids all problems associated with an earlier species-richness weighted mingling index. M_i^o also recognises more different mingling situations and modifies less M_i values. New species mingling index M_i^o puts more weight on the actual process of species mingling rather than on local species richness. In addition, devaluation-strength parameter h allows for a flexible adaptation of the index to further counterbalance the influence of species richness. The influence of parameter h on community and population characteristics is comparatively small, therefore the exact choice is not critical. For the appeal afforded by the simplicity of Eq. (6), analysts may prefer this special case of M_i^o involving a mild devaluation caused by $h = 1$. In any case, it is recommended to use the same value of h when comparing the results from different research plots and to state the selected value of h in publications. We generally recommend the use of index M_i^o in diverse ecosystems where it is important that mingling also takes the recurrence of species in local neighbourhoods into account.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors did not use any AI or AI-assisted technologies.

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Data accessibility statement

The data will be made available on request. R scripts can be obtained from AP.

CRediT authorship contribution statement

Arne Pommerening: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Aila Särkkä:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis.

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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Data availability

Data will be made available on request.

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