Global Ecology and Conservation 46 (2023) e02604

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Complementarity of community indices in characterizing aquatic macroinvertebrate assemblages

Jip de Vries [a,b], Michiel H.S. Kraak [a], Piet F.M. Verdonschot [a,b,*]

[a] *Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands*
[b] *Wageningen Environmental Research, Wageningen UR, P.O. Box 47, 6700 AA Wageningen, the Netherlands*

ARTICLE INFO

Keywords:
Index
Diversity
Species richness
Macroinvertebrates
Indicator species
Rare species

ABSTRACT

Community indices are commonly used in ecology to characterize and track species assemblages. However, their use is also critically discussed. Unclarities remain about what the various community indices actually represent, their appropriateness in representing ecological status, and their drawbacks. Therefore, the present study aimed to elucidate the context-specificity of aquatic macroinvertebrate community index scores in lotic and lentic water bodies. To this end, a large set of macroinvertebrate distribution data in surface waters of the Netherlands was analysed. Five indices were considered, including the diversity indices species richness, Shannon diversity, and Simpson diversity, and two diagnostic indices, the number of rare species and the number of indicator species. Patterns in index scores were compared between lotic waters, lentic waters, and the combined dataset. We observed that the correlation between index scores was not as strong as often assumed. In addition, patterns in index scores differed between lotic and lentic waters, with deviating ranges in scores. These results showed that the interpretation of the patterns in macroinvertebrate community indices scores is dependent on the water type. This highlights the importance of reporting multiple community index scores and of careful interpretation of their meaning within the appropriate context. This should be considered to make appropriate choices in the use of these indices in future water quality assessment and environmental management.

1. Introduction

Diversity indices are widely used to characterize species assemblages and to track how these assemblages develop in a dynamic environment over time. A search on the Web of Science showed that about half of all publications on macroinvertebrate communities in freshwater studies made use of some kind of diversity indices. More specific, the 10 indices most commonly used to quantify the diversity of species and communities, are based on the features richness, diversity and evenness, applied on local to global scales (Koperski, 2011; Magurran and McGill, 2011). Species diversity indices take both the number of species (species richness) and the distribution of the number of individuals of each of these species within a community (evenness or equitability) into account. But the boundary of a community in space, time, and the taxonomical groups incorporated, as well as the different relative weights assigned to species abundances varies. Furthermore, both the definition of community boundaries and the species abundance weights are largely

* Corresponding author at: Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands.
E-mail address: piet.verdonschot@wur.nl (P.F.M. Verdonschot).

https://doi.org/10.1016/j.gecco.2023.e02604
Received 11 April 2023; Received in revised form 20 July 2023; Accepted 10 August 2023
Available online 12 August 2023
2351-9894/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

subjective. Yet, the application of diversity indices in research and management is ongoing without a clear understanding of their ecological meaning. A better understanding of the usefulness of these widely applied indices would thus assist future interpretations.

Richness indicates the number of species (S) or taxa present. Diversity indices combine a measure of richness with evenness in abundance, representing the heterogeneity of an assemblage, like two of the most commonly used indices, the Shannon (H') and Simpson (D) diversity (Magurran and McGill, 2011). The three indices S, H' and D can all be derived from a single generalized entropy formula, known as the Hills series (Hill, 1973; Morris et al., 2014) and are thereby mutually dependent. The different diversity indices range from those with a higher sensitivity to the occurrence of rare species (S) towards a sensitivity to the occurrence of abundant species (D).

In addition to these diversity indices, diagnostic indices like rarity and indicator species are frequently used to further refine assemblage characterisations. Rarity, here defined as species occurring at a few sites in low or high numbers (limited distribution range; Nijboer and Verdonschot, 2004), is central to environmental management and is for instance used in selecting locations with a high conservation value (Boon, 2000; Magurran and McGill, 2011). This type of index can be expressed as the proportion of singletons, or the number of species with low abundances (R). Indicator species, defined as species with characteristics that are assumed to respond to the presence or absence of specific abiotic and biotic factors (Dauvin et al., 2010). Consequently, they may be indicative of environmental quality, integrating its variability over time, and indicating trends (Diekmann, 2003; Niemi and Mcdonald, 2004). Hence, indicator species can be used to diagnose the responses of assemblages to environmental pressures, that are not expressed by diversity indices. Diagnostic indices are therefore commonly and frequently applied in water quality assessment and management.

Despite the widespread application of various community indices in ecology and environmental management, the intended context-specific meaning of the index scores often remains unclear (Hamilton, 2005). This is at least partly due to the nature of the community indices, attempting to describe the complexity of an assemblage in a single value, while the index scores actually depend on the nature of the community index, as well as on the features of the studied communities. Moreover, there is no agreement on which index is more appropriate or informative (Morris et al., 2014), which is further complicated by their mutual dependency. One reason for variation in index scores is their strong dependence on the scale of observation: locally, diversity might be positively impacted by a moderate change in the environment, that acts negatively on a larger scale (Koperski, 2011), or vice versa. Furthermore, three of the selected indices, the number of species, Shannon and Simpson diversity are measures of biodiversity, which are assumed to be study area independent. In addition, we selected two study area specific indices, rarity and the number of WDF indicator species. Most of the other area specific indices, like the country specific IBI's developed for e.g., UK, SP and BE, do not comply with the present study area. In addition, community indices are also used to compare locations, without acknowledging that the ranges of the selected indices might differ strongly between ecosystem types and geographical regions, and hence, differences in species assemblages do not necessarily point at differences in ecological status. Given these uncertainties and debates, many studies have stressed to be careful in the selection and reporting of community index scores (Cazzolla Gatti et al., 2020; Hamilton, 2005; Morris et al., 2014; Stirling and Wilsey, 2001).

Hence, although community indices are among the most frequently used indices in ecology, there is still substantial debate and controversy about the context-specific meaning of the index scores. Therefore, the aim of the present study was to elucidate the context-specific patterns in aquatic macroinvertebrate community index scores in lotic and lentic water bodies. The availability of an extensive dataset of the macroinvertebrate distribution in Dutch surface waters offered the unique possibility to meet this aim. To this end, we compared patterns in the scores for commonly used indices for expressing species diversity and ecological status, both within the specific context of a water type as well as for a large-scale dataset of multiple water types covering the entire country. Hereby, making advantage of a unique large data set, we incorporated all approximately 25 water types in the Netherlands, lentic and lotic, which have been demonstrated to be representative for the NW-European plane (Verdonschot and Nijboer, 2004; Knotters et al., 2010; Verdonschot et al., 2012). In addition, we explored how the selected indices were related. We used the performance of the indices and their mutual responses to evaluate our hypothesis that indices are context-specific and mutually dependent. Finally, we made recommendations for their practical use for water quality assessment. A more thorough understanding of the meaning, context-specificity and relatedness of the scores of these commonly used indices allows to make appropriate choices in the selection of indices, both in ecological research as well as in environmental management.

2. Methods

For the present study, a large dataset was explored that contains macroinvertebrate distribution data for the entire Netherlands. Verdonschot et al. (1992) showed that the Dutch Delta is rich in water types hosting a high macroinvertebrate diversity representative of the N.W. European plain. The data was collected from 2007 to 2016 as a part of the regular ecological monitoring programmes of the Dutch regional water authorities in most of the water types. Only samples collected with the same sampling protocol were used. Aquatic macroinvertebrates were collected by sweeping a 0.5-mm mesh hand-net (width 0.25 cm) through the main habitats (generally five to ten) present in the water body, like submerged vegetation, leave packages and different sediment types. Each habitat was sampled several times over a distance of 0.5–1 m until a total of 5 m was reached. To increase the uniformity of the data and to avoid overlap between taxonomic units, only species-level data was considered, excluding taxa identified on a higher taxonomic level (Nijboer and Verdonschot, 2000). The selected data consisted of 620 lotic and 770 lentic sampling sites, which contained abundance data for 1165 macroinvertebrate species.

For each site, we calculated three commonly used diversity indices: number of species (S), Shannon diversity (H') (Shannon and Weaver, 1964) and Simpson diversity (D) (Simpson, 1949). We also determined the number of rare species (R), according to the Dutch species rarity list for macroinvertebrates (Nijboer and Verdonschot, 2004), as well as the number of indicator species (Ind) according to the Dutch WFD application (van der Molen et al., 2018). In the present study indicator species were defined as those species with a high preference for either flow or stagnation (De Cáceres et al., 2010). To this end, to each species a score was assigned, ranging from a low (1) to a high (5) preference for increased flow velocity according to Verberk et al. (2012). Species with an affinity score of < 1.5 were selected as indicator species for lentic waters, while those with an affinity score of > 4.5 were considered to be indicative of lotic waters.

To assess the relationships between the selected community indices, we performed Spearman correlations between all indices for the complete dataset, and for lotic and lentic waters separately. Next, we evaluated the relationship between the indices in more detail, except indicator species for all sites as these are water type specific. To this end, we plotted each combination of indices in correlation matrices for all sites, and lentic and lotic sites separately. In each plot we distinguished four quadrants. Herewith, the sites were grouped into each of the four quadrants based on the values calculated for the respective pair of indices. The quartile in the low-left contains sites that shows low values for each index considered, the quartile in the high-left contains sites that had low numbers for the index on the horizontal axis and high ones for the index on the vertical. The reverse is applicable for the low-right and high-right quartile, respectively.

Whereas correlation coefficients only show to which degree an association between mean values is monotonic, quantile regressions can show how the tails of the distribution in one variable are dependent on changes in another variable. In other words, in this way it can be tested whether a variable sets limits or constraints to the response of another variable (Downes, 2010). To test this tail-dependency, for each combination of these three indices, associations were tested between the lowest and highest quartile of one variable with a second. For the analysis, we used the R with package quantreg (Koenker et al., 2020).

3. Results

3.1. General patterns in community index scores

For the complete dataset four indices were plotted in a matrix (Fig. 1). The strength of the correlations between these indices varied strongly. For the Shannon (H') and Simpson diversity (D) the association was strongest ($\rho = 0.96$). However, comparing these indices with the number of species (S) showed a less clear pattern. Although these indices were still strongly correlated ($\rho = 0.73$, $\rho = 0.62$), for lower species numbers, a wide range of Shannon and Simpson index scores occurred. No clear associations were found between the number of rare species and the other indices. The number of indicator species was not included here, because these indicated either flow or stagnation, and as such they are water type dependent which becomes meaningless on the scale of an entire country where both lotic and lentic waters are included.

3.2. Community indices per water type

Lotic waters showed a higher maximum number of species per site ($S_{max,\ lotic} = 133$; $S_{max,\ lentic} = 102$), as well as a higher maximum number of rare species per site ($R_{max,\ lotic} = 44$; $R_{max,\ lentic} = 7$) compared to lentic waters (Fig. 2). Lentic waters showed a higher minimum Shannon and Simpson diversity compared to lotic waters ($H_{min,\ lotic}$=0.07, $H_{min,\ lentic}$=0.68; $D_{min,\ lotic}$=0.02, $D_{min,\ lentic}$=0.21).

Compared to the complete dataset, some patterns became clearer when considered for the separate water types, whereas other associations were less strong. Clearer correlation patterns arose for the complete dataset in comparison to the lotic and lentic waters separately for the association between the number of species and the Shannon and Simpson indices. Also, the association between the number of rare species and the Shannon and Simpson indices was weaker for both water types separately compared to the complete

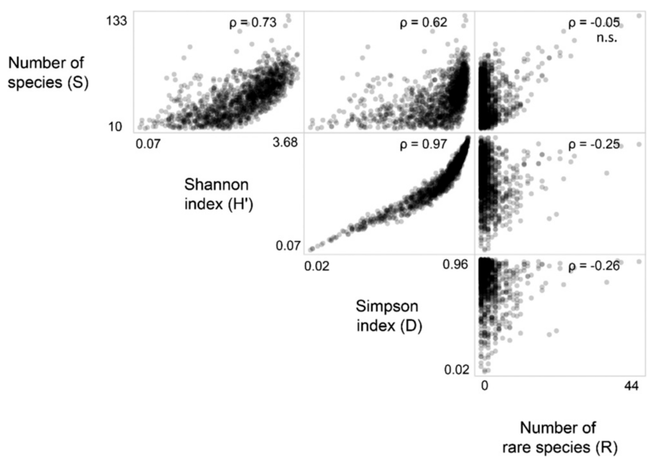

Fig. 1. Correlation matrix for indices indicating macroinvertebrate diversity of sites belonging to lotic and lentic waters in the Netherlands. The top right values indicate Spearman correlations, significant at p = 0.05, unless noted otherwise.

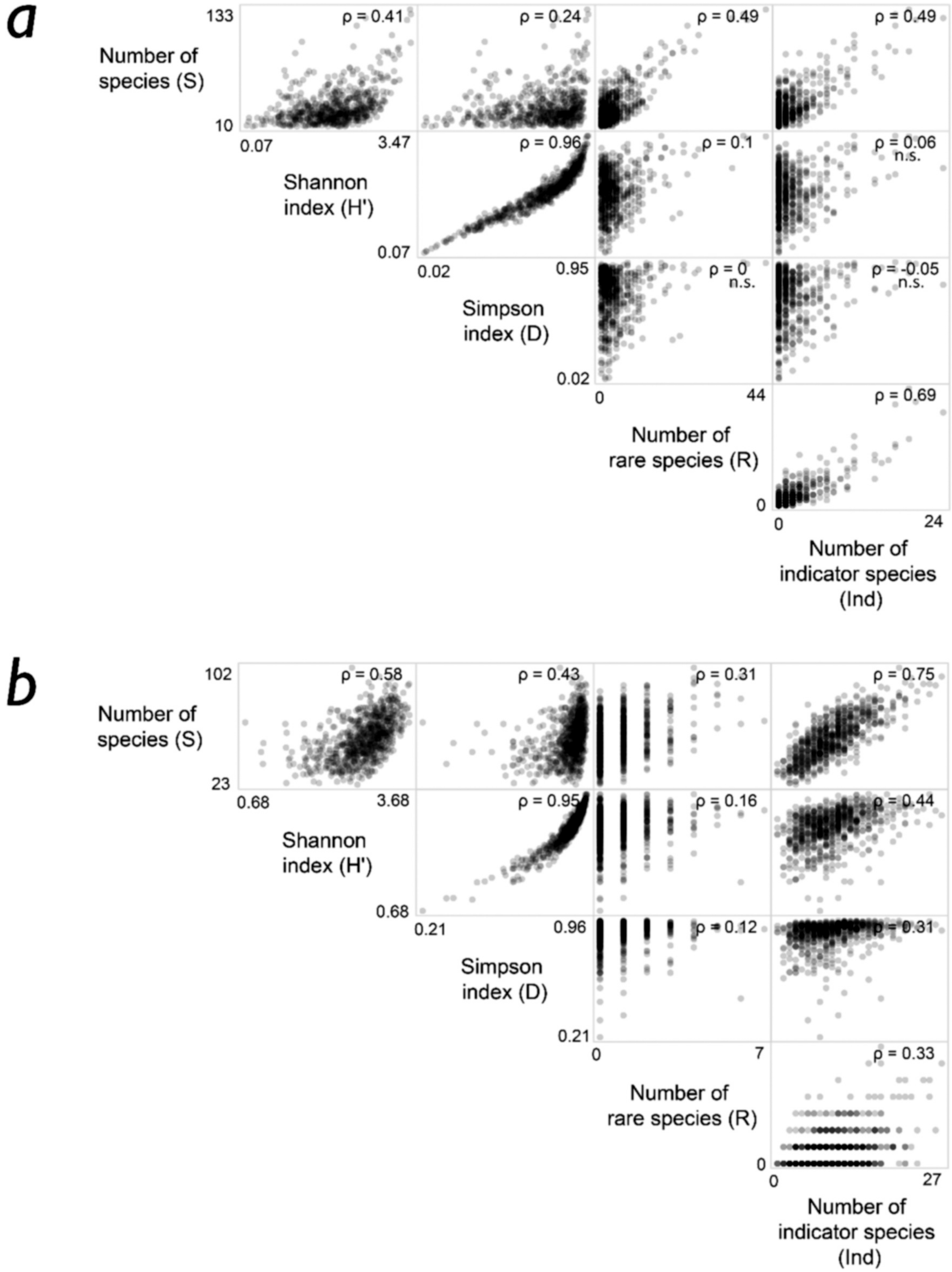

Fig. 2. Correlation matrix for indices indicating macroinvertebrate diversity of sites belonging to lotic (a) and lentic waters (b) separately. Lower half indicates Spearman correlations, significant at $p = 0.05$, unless noted otherwise.

dataset.

Contrastingly, there was a stronger correlation between the number of species and the number of rare species in either the lotic or the lentic waters compared to the complete dataset ($\rho_{lotic} = 0.49$; $\rho_{lentic} = 0.31$; $\rho_{total} = -0.05$ (n.s.)). When comparing the two water types, the association was stronger for lotic waters, where a higher number of species also implied a higher number of rare species, whereas for lentic waters, at a high number of species, the number of rare species still differed strongly.

The number of indicator species could be calculated as an additional index for the two specific water types. The association between the number of species and the number of indicator species was stronger for lentic waters than for lotic waters ($\rho_{lotic} = 0.49$; $\rho_{lentic} =$

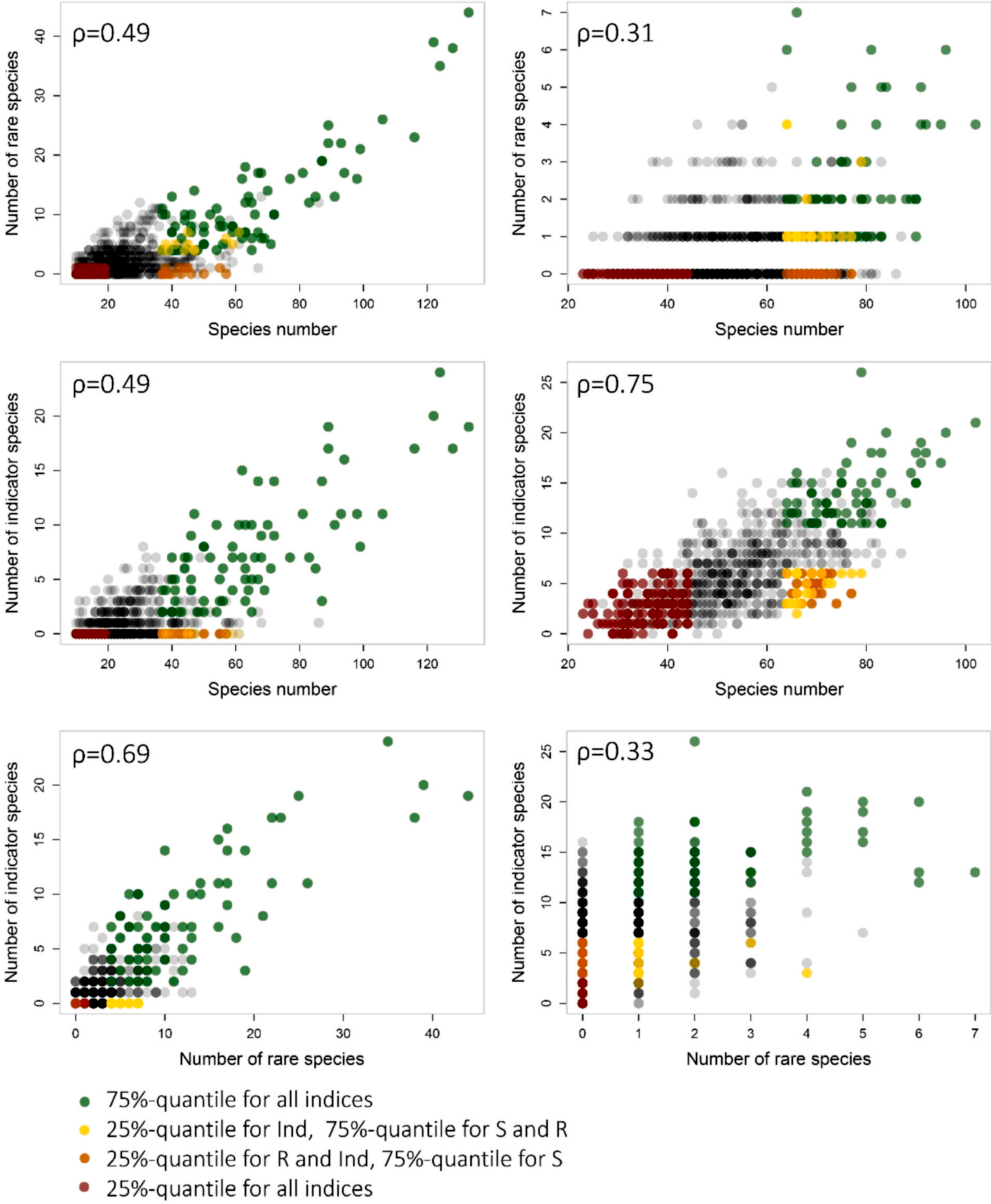

Fig. 3. Scatter plots for combinations of three indices for lotic (three panels on the left) and lentic (three panels on the right) waters. The colour of the dots represent datapoints in the upper and lower quartiles of each index.

0.75). In contrast, the association between the number of rare species and the number of indicator species was stronger for lotic waters ($\rho_{lotic} = 0.69$; $\rho_{lentic} = 0.33$). Associations between the number of indicator species with Shannon and Simpson indices were not significant for lotic waters, but significant for lentic waters.

To evaluate the association between the indices for the four different quartiles or groups of sites based on the values calculated for the number of species, the number of rare species and the number of indicator species, three pairs of plots are shown with the lowest and highest quartiles colour-coded for lentic and lotic waters separately (Fig. 3). These colour-coded groups are delineated by the highest and lowest quartiles of each index and show similar patterns among the combinations of indices for both water types. The large group of sites with low scores for all three indices (marked red) is concentrated in the lower corner of each graph, whereas the group with higher scores for all three indices (marked green) showed a more scattered distribution in the six graphs of Fig. 3. Sites with a high number of species and rare species, but a low number of indicator species (marked yellow and orange) were less numerous and were therefore clustered.

The selected indices were asymmetrically associated, with increasing scatter for higher index values (Fig. 3). This was quantified by calculating the quantile regressions on the lowest ($\tau = 0.1$) and highest ($\tau = 0.9$) quartile of the number of rare species, showing that the lower tail of the distribution of this index was less sensitive to changes in the total number of species than the higher tail of the distribution (Table 1).

4. Discussion

4.1. Complementarity of community indices in characterizing species assemblages

The presently observed patterns in the scores of the selected diversity and diagnostic community indices showed that they all picture different characteristics of species assemblages, and are, therefore, complementary in their informative value. The number of species increases with increasing number of individuals that in turn depends on the interplay between geographical position, habitat type and ecosystem productivity (Srivastava and Lawton, 1998). Hence, especially species richness is sensitive to sampling effort (McGuinness, 1984), and its estimation can thus hinge on how samples are standardized. The Shannon and Simpson indices are more robust than species richness to the number of individuals and to the sampling design (Chao and Jost, 2015; Roswell et al., 2021). The Shannon's index emphasizes the species richness component of diversity, while the Simpson's index emphasizes the evenness component. This means that the Shannon index is more sensitive to the presence of rare species (Chao and Jost, 2015; Roswell et al., 2021) and the Simpson's index to the presence of the more dominant ones. Along with the number of species, for both indices also species abundances are important. As we used unadjusted abundance data, unavoidable uncertainty due to sampling issues may have affected the indices scores. But also sampling timing influences abundances and therewith indices scores, by collecting either many young larvae or lesser individuals of later stages. Hence, although there is a strong positive association between the number of species and the composite indices Shannon and Simpson diversity (Hill, 1973; Stirling and Wilsey, 2001), they cannot be used interchangeably. In the present study this became especially evident at lower numbers of species, where the Shannon and Simpson indices showed strong variability, the more so when considering the lotic and lentic waters separately. These indices are thus less informative at low species numbers and need to be used with care.

The number of indicator species is mainly depending on specific abiotic and biotic environmental conditions and is therefore water type specific. In the present study the number of indicator species correlated to the total number of species, especially in lentic waters. In contrast to the number of indicator species, the number of rare species also depends on characteristics intrinsic to the species itself, like phenology, phylogeny, functional and life history traits, and geographical range size (Gaston, 1994; Cunningham-Minnick et al., 2022). In the present study, lentic waters generally contained less rare species, in line with Nijboer and Verdonschot (2004) who showed large differences in the numbers of rare species between the geographical areas in the Netherlands. This could partly be explained by landscape features of the areas, especially the surface area, a lower variety in water types, the geological age, and the number of near-natural waters. In lotic waters on the other hand, the correlation between the number of species and the number of indicator species was higher. This was due to the high overlap between the list of indicator species and that of the rare species. Both lists are dominated by species that are sensitive to lower oxygen concentrations and low flow and stagnation. In general, rare species have a strong influence on the Shannon index and less on the Simpson index (Roswell et al., 2021). There was indeed a weaker correlation between the Shannon index and rarity in our data. In contrast, more dominant species have a stronger effect on the Simpson index (Roswell et al., 2021). Thus, although lotic waters hosted more rare species, rarity in lotic waters was not related to the Simpson index, as the role of the more dominant species prevailed.

Table 1
Quantile regression slope for index associations as depicted in Fig. 3, for quantiles tau = 0.1 and tau = 0.9. R: number of rare species, S: number of species, Ind: number of indicator species. For regression plots, see Appendix Fig. A1.

Index association	Lotic waters		Lentic waters	
	$\tau = 0.1$	$\tau = 0.9$	$\tau = 0.1$	$\tau = 0.9$
R, S	0.02	0.30	0	0.05
Ind, S	0	0.19	0.19	0.30
Ind, R	0.09	0.80	1.00	2.2

4.2. Drivers of patterns in community index scores

A selection of community indices was calculated for a large number of lentic and lotic waters distributed over different geographical regions in the Netherlands. Different patterns in community index scores appeared when comparing the results of the complete dataset with the lentic and lotic waters separately, both in the range of the index scores as well as in the index associations.

The differences in index score patterns between the lotic and lentic waters might be due to the biogeographical history of freshwater habitats in the study area. The hydromorphological history of the Netherlands is characterized by the interacting factors of limited relief, (sub)surface composition, water quality, and human activities (Berendsen, 2005). Nowadays, lentic waters are present in larger quantities than lotic waterbodies, especially in the form of 330.000 km of drainage ditches (CBS et al., 2009). Lentic and lotic water are characterized by different evolutionary dynamics, where the ephemeral nature of lentic habitats may have increased the mobility and range size of lentic species (Griffiths, 2006; Ribera and Vogler, 2000). In contrast, more permanent lotic habitats will then be inhabited by species specialized to cope with the forces of current and the related oxygen regime, because in lotic waters flow is the main environmental driver of community composition (Poff et al., 1997). Here, species occur that are specialized to live in these running waters, which are often also rare species within the geographical range of the Netherlands, resulting in a strong association between the number of rare species and indicator species for lotic waters. In lentic waters, other and a wider variety of environmental factors are jointly driving the composition of the local assemblage, such as the trophic state, the acidity and the dissolved oxygen concentration (Verdonschot, 1992). Here, less rare species are present and the association between the number of rare and indicator species is not as strong. Hence, this biogeographical and hydromorphological context obviously influenced the observed patterns and relationships between the various indices.

The prevalence of lentic habitats in the Netherlands also influences the perceived rarity of lentic species. National rare species lists do not rank lentic species on high positions, because their habitat is common and abundant, whereas less abundant lotic habitats with associated specialized species result in a higher number of possible rare lotic species. This rarity is thus partly water type related, besides being inherent to the species itself, due to low dispersal capabilities, a low number of offspring or other species specific life history characteristics (Gaston, 1994; Nijboer and Verdonschot, 2004). Based on the present observations it is concluded that the drivers of patterns in community index scores differ between lentic and lotic water bodies, underlining their context specificity. This can be extended to even more specific water types, such as peat pits or intermittent and ephemeral waters, where specific environmental conditions prevail (de Vries et al., 2020). Thus, community indices have a higher ecological relevance within regions and water types, hence within the appropriate context, as also shown by amongst others Verdonschot (1990), Verdonschot and Nijboer (2000) and Verdonschot (2006).

4.3. Effects of ecological water quality on community index scores

Because of the observed complementarity of the presently evaluated community indices, assessment systems should preferably not rely on a single index. This is supported by Chao and Jost (2015), who proposed the simultaneous use of a variety of indices to describe community assemblages, rather than selecting single measures, like the number of species and the Shannon and Simpson index. Morris et al. (2014) compared the performance of combined and single indices to detect the relationships between diversity and traits of organisms, and could indeed not identify an ideal single index, and therefore suggested to report multiple indices. In a conservation context, it has been shown that biodiversity indices are not sufficient to select conservation areas for rare species (Lawler et al., 2003), which, again, suggests the additional value of using multiple indices. The present as well as the previous examples of complementarity indeed invite to calculate multiple indices, but even then, it is needed to consider the meaning of each index individually, as each may answer a different (part of the) question given the context of the sites of interest. The number of species reflects the simple count of all species present and as this number depends on the water type and water quality status it should in any case be compared to a reference situation. The difference between the Shannon and Simpson index is directly related to the weight of the presence and abundances of either rare or dominant species. We showed that in the Netherlands the Shannon index scores higher in lotic waters due to the occurrence of more rare species. But between different geographical areas this can differ and therefore, one should compare both the Shannon as well as the Simpson index with reference sites.

Concerning the scales of the assessments of diversity, our results showed that multiple indices should only be used within a specific geographical region and a specific water type to increase mutual comparability which is in line with previous studies (Verdonschot, 1990; Nijboer and Verdonschot, 2004; Nijboer and Schmidt-Kloiber, 2004; de Vries, 2021). Also, when tracking the effects of management measures or in diagnostic monitoring of water quality, the complementarity of community indices should be considered, because each index may differently influence the decision on which measures to be taken. Hence, especially in the practice of water management, calculating a variety of community indices is highly recommended, to avoid misinterpretations of data and wastes of financial investments in ecosystem restoration.

In addition to geography and water type, ecological water quality was considered to be the third main environmental driver of our data. It might have been expected that with increasing ecological water quality, each index score would have increased independently, and so would have the combinations of index scores. The present study distinguished four groups of sampling sites with different combinations of index scores, and indeed, the largest part of the sites was found in either the lower or the higher corner of the graphs, indicating either low or high values for all selected indices. Sites with low values for each index might indicate disturbed sites with a low ecological water quality, and a few dominant, generalist species. In the most optimal case, reflecting a high ecological quality, all three indices score high. These sites are characterized by specific environmental conditions and are otherwise less disturbed, which will enhance the presence of a high number of specialist and rare species. However, for a substantial number of sampling sites the index scores showed more or less scatter, depending on the community index combination. Such sites contained a relatively high number of species, but a low number of rare and indicator species. This might indicate an abundant presence of waters with moderate environmental conditions and a high ubiquist species diversity. Hence, many of the species that are abundant in the Netherlands may be found here. An increasing number of rare species may then be indicative of less abundant water types, which are, however, still not very selective in terms of specific environmental conditions. Hence, such situations may point at either ecologically unusual conditions, or at a bias in sampling. In contrast, most sites followed a different trajectory, where the number of rare species increased along with the number of indicator species. These species might also partly overlap being both rare and indicative, as the specific environments in which indicator species occur are also less abundant. The presently observed effects of ecological water quality on the community index scores and their (lack of) interdependence emphasizes the need to combine several indices for diagnostic monitoring to fuel restoration measures.

5. Conclusions

The present study aimed to elucidate the context-specific patterns in aquatic macroinvertebrate community index scores in lotic and lentic water bodies. The observed patterns in the scores of the selected community indices showed that they all picture different characteristics of species assemblages, and are, therefore, complementary in their informative value. Hence, especially in the practice of water management, calculating a variety of community indices is highly recommended, to avoid misinterpretations of data and wastes of financial investments in ecosystem restoration. Also the drivers of patterns in community index scores differed between lentic and lotic water bodies, underlining their context specificity. Thus, community indices have a higher ecological relevance when used within regions and water types, hence within the appropriate context. This should be considered to make appropriate choices in the use of these indices in future water quality assessment and environmental management.

CRediT authorship contribution statement

JdV, **MK** and **PFMV** designed the study. **JdV** and **PFMV** collected the data and performed the analyses. **JdV**, **MK** and **PFMV** wrote most of the manuscript together. **PFMV** and **MK** advised on practical issues during the course of the study and data processing and contributed to editing and revising draft versions of the manuscript.

Declaration of Competing Interest

The authors declare no competing interests.

Data Availability

Data will be made available on request.

Acknowledgements

This research was part of the Stroomgebiedsbrede Ecologische SysteemAnalyse Methode (SESAM) project, funded by the Dutch Foundation for Applied Water Research (STOWA) and five Dutch water authorities (Waterschap Rivierenland, Waterschap Limburg, Waterschap Vallei & Veluwe, Waterschap Aa & Maas, Hoogheemraadschap Hollands Noorderkwartier). We thank the water authorities for kindly providing us with their monitoring data.

Author contributions

All authors contributed to the design. JV performed data analysis. JV wrote the manuscript, and PV and MK contributed to the review and revision. All authors gave final approval for publication.

Appendix

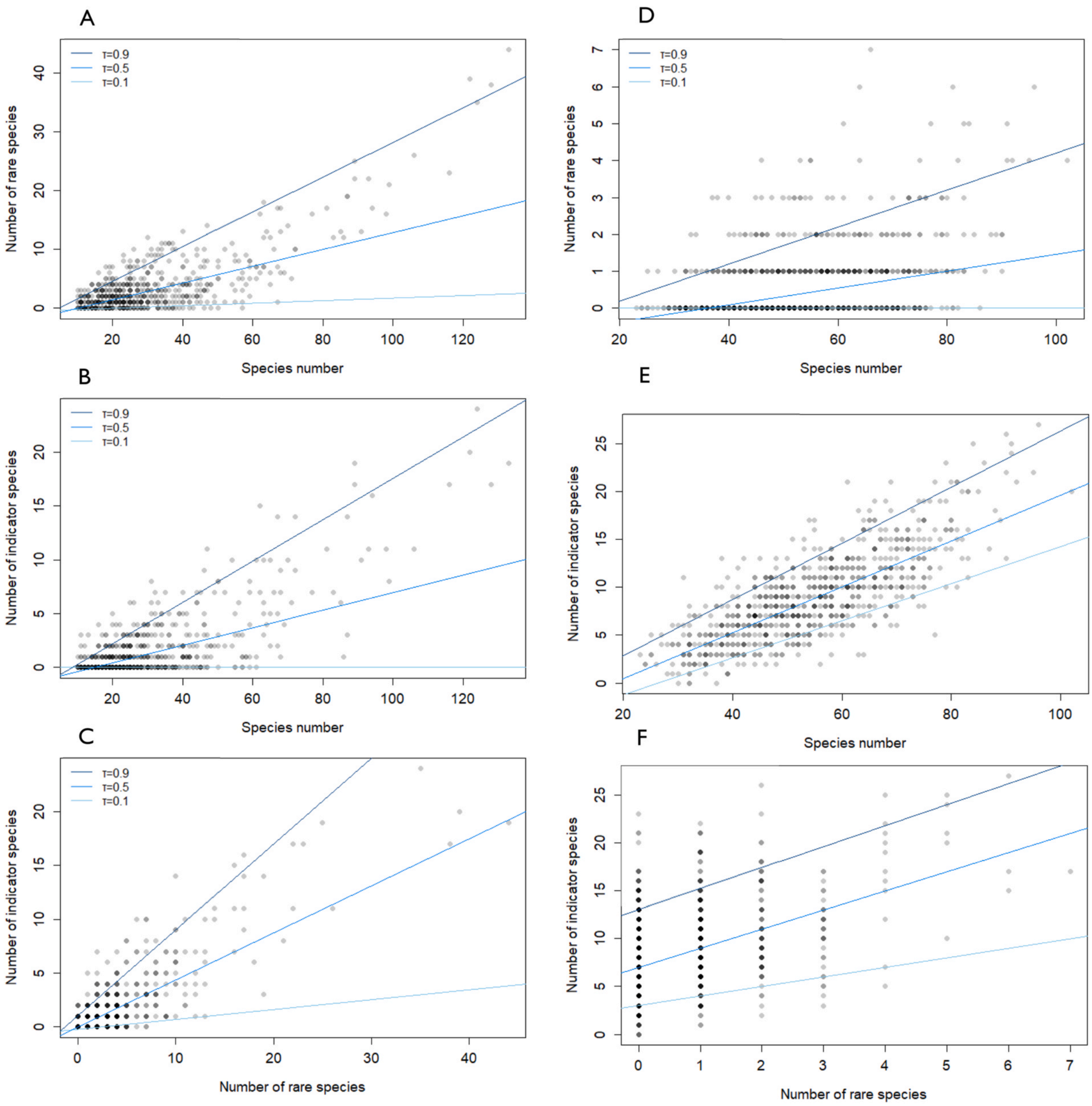

Fig. A1. Quantile regression plots for lotic (left) and lentic waters, for three indices (S, R, Ind).

.

References

Berendsen, H.J.A., 2005. Landschap in delen. Overzicht van de geofactoren. Van Gorcum, Assen.

Boon, P.J., 2000. The development of integrated methods for assessing river conservation value. Hydrobiologia 422–423, 413–428. https://doi.org/10.1007/978-94-011-4164-2_32.

Cazzolla Gatti, R., Amoroso, N., Monaco, A., 2020. Estimating and comparing biodiversity with a single universal metric. Ecol. Modell. 424, 109020 https://doi.org/10.1016/j.ecolmodel.2020.109020.

CBS, PBL, RIVM, WUR, 2009. Oppervlaktewater in Nederland [WWW Document]. Compend. voor Leefomgeving. URL ⟨https://www.clo.nl/indicatoren/nl140101⟩ Links.

Chao, A., Jost, L., 2015. Estimating diversity and entropy profiles via discovery rates of new species. Methods Ecol. Evol. 6, 873–882. https://doi.org/10.1111/2041-210X.12349.

Cunningham-Minnick, M.J., Milam, J., King, D.I., 2022. SpORtI: The species originality and rarity index combines phylogenetic and functional originality with rarity metrics to provide a new perspective on species rarity. Ecol. Indic. 143, 109339.

Dauvin, J.C., Bellan, G., Bellan-Santini, D., 2010. Benthic indicators: From subjectivity to objectivity - Where is the line? Mar. Pollut. Bull. 60, 947–953. https://doi.org/10.1016/j.marpolbul.2010.03.028.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119 (10), 1674–1684.

Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology - A review. Basic Appl. Ecol. 4, 493–506. https://doi.org/10.1078/1439-1791-00185.

Downes, B.J., 2010. Back to the future: Little-used tools and principles of scientific inference can help disentangle effects of multiple stressors on freshwater ecosystems. Freshw. Biol. 55, 60–79. https://doi.org/10.1111/j.1365-2427.2009.02377.x.

Gaston, K.J., 1994. Rarity, Population and Community Biology Series.

Griffiths, D., 2006. Pattern and process in the ecological biogeography of European freshwater fish. J. Anim. Ecol. 75, 734–751. https://doi.org/10.1111/j.1365-2656.2006.01094.x.

Hamilton, A.J., 2005. Species diversity or biodiversity? J. Environ. Manag. 75, 89–92. https://doi.org/10.1016/j.jenvman.2004.11.012.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences author (s): m. o. hill published by: ecological society of america diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Knotters, M., Lahr, J., Van Oosten-Siedlecka, A.M., & Verdonschot, P.F.M. 2010. Aggregation of ecological indicators for mapping aquatic nature quality: overview of existing methods and case studies (No. 209). Wettelijke Onderzoekstaken Natuur & Milieu.

Koenker, R., Portnoy, S., Ng, P.T., Melly, B., Zeileis, A., 2020. Package "quantreg."

Koperski, P., 2011. Diversity of freshwater macrobenthos and its use in biological assessment: a critical review of current applications. Environ. Rev. 19, 16–31. https://doi.org/10.1139/A10-023.

Lawler, J.J., White, D., Sifneos, J.C., Master, L.L., 2003. Rare species and the use of indicator groups for conservation planning. Conserv. Biol. 17, 875–882. https://doi.org/10.1046/j.1523-1739.2003.01638.x.

Magurran, A.E., McGill, B.J., 2011. Part II - diversity. In: Biological Diversity. Oxford University Press.

McGuinness, K.A., 1984. Species–area curves. Biol. Rev. 59 (3), 423–440.

Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., Rillig, M.C., 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecol. Evol. 4, 3514–3524. https://doi.org/10.1002/ece3.1155.

Niemi, G.J., Mcdonald, M.E., 2004. Application of ecological indicators. Annu. Rev. Ecol. Syst. 35, 89–111. https://doi.org/10.1146/annurev.ecolsys.35.112202.130132.

Nijboer, R.C., Schmidt-Kloiber, A., 2004. The effect of excluding taxa with low abundances or taxa with small distribution ranges on ecological assessment. Integrated Assessment of Running Waters in Europe. Hydrobiologia 347–363.

Nijboer, R.C., Verdonschot, P.F.M., 2000. Taxonomic adjustment affects data analysis: an often forgotten error. Int. Ver. für Theor. und Angew. Limnol. Verh. 27, 2546–2549.

Nijboer, R.C., Verdonschot, P.F.M., 2004. Rare and common macroinvertebrates: definition of distribution classes and their boundaries. Arch. Hydrobiol. 161, 45–64.

Poff, N.L.R., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime: a paradigm for river conservation and restoration. Bioscience 47, 769–784. https://doi.org/10.2307/1313099.

Ribera, I., Vogler, A.P., 2000. Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. Biol. J. Linn. Soc. 71, 33–52. https://doi.org/10.1006/bijl.1999.0412.

Roswell, M., Dushoff, J., Winfree, R., 2021. A conceptual guide to measuring species diversity. Oikos 1–18. https://doi.org/10.1111/oik.07202.

Shannon, C.E., Weaver, W., 1964. The mathematical theory of communication. Int. Bus. 8, 21–33.

Simpson, E.H., 1949. Measurment of diversity. Nature 688, 688.

Srivastava, D.S., Lawton, J.H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am. Nat. 152 (4), 510–529.

Stirling, G., Wilsey, B., 2001. Empirical relationships between species richness, evenness, and proportional diversity. Am. Nat. 158, 286–299. https://doi.org/10.1086/321317.

van der Molen D.T., Pot R., Evers C.H.M., van Herpen F.C.J. & van Nieuwerburgh L.L.J. (2018). Referenties en maatlatten voor natuurlijke watertypen voor de Kaderrichtlijn Water 2021–2027 (No. 2018–49). Stowa.

Verberk, W.C.E.P., Verdonschot, P.F.M., Haaren, T. van, Maanen, B.Van, 2012. Milieu- en habitatpreferenties van Nederlandse zoetwater- macrofauna: WEW Themanummer 23.

Verdonschot, P.F.M. 1990. Ecological characterization of surface waters in the province of Overijssel, The Netherlands. Wageningen University and Research.

Verdonschot, P.F.M., 1992. Macrofaunal community types of ditches in the province of Overijssel (The Netherlands). Archiv für Hydrobiologie. Supplementband. Untersuchungen des Elbe-AEstuars, 90 (2), 133–158.

Verdonschot, P.F.M., 2006. Data composition and taxonomic resolution in macroinvertebrate stream typology. Hydrobiologia 566, 59–74.

Verdonschot, P.F.M., Nijboer, R.C. 2000. Typology of macrofaunal assemblages applied to water and nature management: a Dutch approach. In Assessing the biological quality of fresh waters: RIVPACS and other techniques. Proceedings of an International Workshop held in Oxford, UK, on 16–18 September 1997 (pp. 241–262). Freshwater Biological Association (FBA).

Verdonschot, P.F.M., Nijboer, R.C., 2004. Testing the European stream typology of the Water Framework Directive for macroinvertebrates. Integrated assessment of running waters in Europe. Hydrobiologia 35–54.

Verdonschot, P.F.M., Higler, L.W.G., Van der Hoek, W.F., Cuppen, J.G.M., 1992. A list of macroinvertebrates in Dutch water types: a first step towards an ecological classification of surface waters based on key factors. Hydrobiol. Bull. 25, 241–259.

Verdonschot, R.C., Keizer-Vlek, H.E., Verdonschot, P.F.M., 2012. Development of a multimetric index based on macroinvertebrates for drainage ditch networks in agricultural areas. Ecol. Indic. 13 (1), 232–242.

de Vries, J. 2021. Biology-based approaches to unravel multiple stressor impacts on aquatic ecosystems.Thesis, University of Amsterdam.

de Vries, J., Kraak, M.H.S., Verdonschot, R.C.M., Verdonschot, P.F.M., 2020. Species composition drives macroinvertebrate community classification. Ecol. Indic. 119, 106780 https://doi.org/10.1016/j.ecolind.2020.106780.