

Morpho-ecospaces, or how to measure biodiversity in a different way

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Abstract

The current biodiversity crisis warrants accurate measuring of biodiversity, often achieved by counting species or higher taxonomic units, with morphological or molecular methods. Alternatively, trait-centred approaches categorise organisms into distinct ecological roles and then count the number of occupied roles to measure biodiversity. Even combinations of trait-based and taxonomic approaches are utilised. However, when investigating the theoretical aspects, all these approaches have significant shortcomings, which complicate a reliable biodiversity measurement, that is, the ignorance of polymorphic species, the sensitivity to the initial classification or the knowledge gap concerning the ecology of the organisms. We outline a non-discrete ecospace approach for which neither pronounced taxonomic expertise nor in-depth knowledge about the ecology of the organisms is required. A morphospace based on quantitative morphological properties is used as a proxy for an ecospace, thus resulting in a continuous morpho-ecospace. With this, decision-making concerning taxonomy or ecology is reduced, as morphology is directly used instead of being first interpreted. Differences usually not considered due to polymorphism or ontogeny can be included in this approach, as well as fossils without species determination. This morpho-ecospace approach is easily applicable and can be combined with already existing approaches, making it broadly applicable.

KEYWORDS

biodiversity, biological traits, biomonitoring, diversity indicators, diversity proxy

1 | BACKGROUND

1.1 | Objective: Improving measures of evaluating biodiversity

In the age of a changing environment, the loss of biodiversity is a major threat to humankind. To recognise

such losses, tools for measuring biodiversity and its changes are necessary. Hence, monitoring biological diversity on multiple levels is a cornerstone in modern public health, pest control in agriculture, water management and conservation programs (Bartram & Ballance, 1996; Mei et al., 2012; Needham et al., 2007; Woodward et al., 2010; Yoccoz et al., 2001). Modern

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biomonitoring is directed towards inferring the changes in the environment, often based on observing changes in species richness and species diversity within biological communities in time and space (Birk et al., 2012). This approach has not changed with the application of high-throughput molecular methodologies such as next-generation sequencing (NGS) and metabarcoding (Beermann et al., 2018; Elbrecht & Leese, 2015). Ultimately, such monitoring approaches form the basis of political decisions (Wilson et al., 2006).

We will outline the shortcomings of three common approaches of measuring biodiversity and point out that there is in fact a significant gap in this area of research, supporting earlier evaluations (e.g. Spaak et al., 2017). Based on the recognised practical and conceptual shortcomings, we will propose how a different, or at least additional approach of measuring biodiversity could look like.

1.2 | A short note on terminology

When describing and discussing the ecological properties of species, we face a common challenge: language. One aspect to be considered in this context is the term 'niche'. The niche is in principle a small area in a large multi-dimensional ecological space, describing the autecology of a single species and its biotic interactions with other areas of the occupied multi-dimensional space (Hutchinson, 1957; Sexton et al., 2017). In the strict view, the niche itself is therefore always directly associated with this specific species ('realised niche'). However, the term 'niche' has also commonly been used to address a principal ecological function (factually also a part of a larger multi-dimensional ecospace), which is not necessarily coupled to a specific species ('potential niche'). In principle, this is a 'niche sensu lato'. The difference in use becomes immediately apparent in the expression 'unoccupied niche'. This term makes no sense in the strict application, where a niche is coupled to a specific species, but only in the second, wider sense, describing cases where a certain ecological function known from one community is not present in another one.

In the absence of a better term, we have to use the term 'niche' in its wider meaning as well, as we make theoretical cases comparing communities. Although this might be seen critical by some readers, we feel currently unable to come up with an alternative term to describe a discrete part of an ecological space in a theoretical discussion. This statement is necessary to avoid any possible misunderstandings concerning the

following discussion. With the ground rules of the terminology set, we will point out three examples, showing inadequacies of the methods we use to measure biodiversity and its changes.

2 | EXAMPLE 1, TAXONOMY-CENTRED APPROACHES: DIVERSITY INDICES

2.1 | Taxonomy as a proxy for biodiversity

Diversity indices are an important measure of existing biodiversity and the rate of its change in modern ecology and biodiversity research, but also in conservation biology (Huang et al., 2016; Mshvildadze et al., 2010; Villéger et al., 2008). They are most readily applied to the diversity of the organisms of a single habitat or biotope ('community'), or generally in alpha diversity studies (Jost, 2007). They basically summarise the diversity within a community into a single value which then can be compared, for example, between different communities or for the same community at different times. With this function, diversity indices have become important in conservation biology and represent a crucial evaluating tool in times of drastic environmental change and the biodiversity crisis in general (Dirzo et al., 2014; van Klink et al., 2020).

Typical examples for alpha diversity measures are the Simpson index (Simpson, 1949) or the Shannon Index (also known as Shannon-Wiener Index or Shannon-Weaver Index; Keylock, 2005; Shannon, 1948; Spellerberg & Fedor, 2003). Different indices differ in sensitivity for specific aspects: the Simpson Index, for example, is more sensitive to species richness, that is, the mere number of species, while the Shannon Index is more sensitive to species evenness, that is, the relative number of individuals per species (Keylock, 2005).

Despite these differences in sensitivity, all such types of diversity indices factually measure taxonomic properties of a community, by counting species or in some cases also supra-specific taxonomic units. As this counting of species requires first the identification of species, the 'archaic-appearing' field of taxonomy has become an important scientific field of research. Taxonomy is back, contributing significantly to other fields of science such as diversity research, ecology and conservation biology due to its relation to diversity indices (Carvalho et al., 2005; Engel et al., 2021).

It is a common strategy to use base assumptions to simplify complex observations. Diversity indices also fall into this category. The weakness of this approach results from

the base assumptions behind these simplifications outlined in the following.

2.2 | The general niche width problem

For exploring the base assumptions behind diversity indices, we will look at simplified hypothetical communities with very few components and sometimes extreme properties to demonstrate in which aspects common indices lack sensitivity. We will think of these as entities in a multi-dimensional ecological space or ecospace (e.g. Bambach et al., 2007). First, we need to recognise that here, species are used as proxies for ecological properties, without assigning traits. When counting species, these represent discrete entities that are all of the same size (or value), as each species is one count (although it is weighed differently in the formulae of the different indices). Why is this approach problematic concerning ecological properties?

We assume a hypothetical community A, which contains ten species. Each species is represented in the community by a similar number of individuals. All ten species occupy comparably narrow niches. In another community B, we have only five species, again all represented by a similar number of individuals, but these species occupy comparably broad niches. In both cases, the same 'ecological space' may be filled as each niche of one of the five species of community B roughly equals the niches of two of the ten species of community A (Figure 1).

In such a case, most diversity indices would indicate that the community containing more species is twice as diverse as the other one. From a conservation biological point of view, this case is not as simple, as both communities are similar concerning their ecological space. Which leads to the question, whether it is more important to protect communities with species that have narrow niches rather than those with broad niches? One could argue that it could be ecologically more sustainable in the long run to choose to protect communities with species with

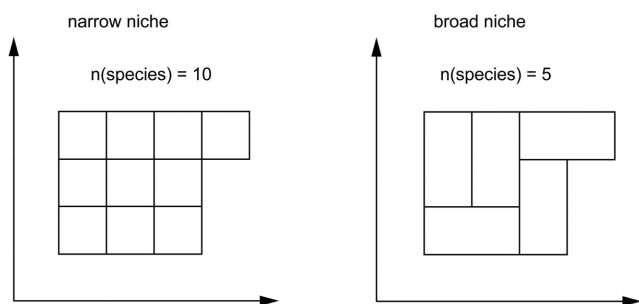


FIGURE 1 The niche width problem. A lower number of species (right) may occupy the same ecospace as a larger number of species (left).

comparably broader niches. Yet, this view may be oversimplified as well.

To emphasise this in a monitoring aspect: When assessing the functional state of two communities, which one do we consider functionally more diverse? It is entirely possible that community A (10 species) contains more specialists, but community B (five species) with broader niches may provide more diverse ecosystem functions and therefore provide more ecosystem services (which is relevant also for human wellbeing). In principle, this effect is stronger in the Simpson Index, but also affects the Shannon Index. There will be also other differences between the communities. More species will mean more interactions and more dependencies on a community. This could indicate that a community with more species may have more 'weak spots'. Yet, so far diversity measures have not considered aspects of interdependencies in a community.

One could assume that this 'niche width problem' would relate to a simple generalist-versus-specialist problem: specialists having narrow niches, generalists having comparably broader niches. The case is much more complex though, relating to numerous different aspects of biology, further outlined in the following.

2.3 | Niche width problem: Polymorphism

A broad niche of a species may be coupled to the fact that the niche of each individual is very broad, but very similar among all individuals. Yet, it is also possible that the niche of each individual is narrow, being highly specialised, but the different individuals of the species differ remarkably from each other, that is, the species is strongly polymorphic (Figure 2). This polymorphism may be caused, for example, by genetic variability or by phenotypic plasticity.

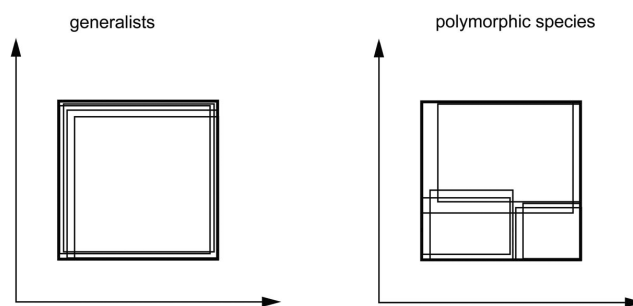


FIGURE 2 Generalist vs. polymorphic species, or how do the individuals of a species contribute to the occupied ecospace. All individuals may occupy almost identical regions of the ecospace (left). Alternatively, individuals may occupy smaller areas, but differ in their position, overall occupying the same area as in the first example (right).

What does this mean for a community? If we look at the famous example of the Darwin finches (Darwin, 1841; Grant, 1999; Lack, 1947), is it really 'relevant' in an ecological context that we have numerous different species with different beak shapes? One could instead argue that the real important aspect is the ecological and morphological diversity. If we have a similar community, but several of these forms represent fewer, but strongly polymorphic species, the common diversity indices would be significantly lower (Figure 3), while the occupied ecological space would be the same. Does the lower index indeed reflect an ecological difference between such two hypothetical communities? These thoughts likewise reveal the weakness of the assumption that the number of species is a good proxy for the functional diversity of a community, which does not seem to be the case (Mlambo, 2014).

2.4 | Niche width problem: Larval diversity

But the niche width problem is even more complex. The ontogeny of species within a community can play an important role in this respect. Species lacking discrete larval forms (see Haug, 2020 for challenges of the term) seem to occupy about the same ecological niche throughout their entire post-embryonic ontogeny (although significant differentiation related to size changes can occur; Benson et al., 2014). Yet, in species with a pronounced larval phase, the larvae often occupy a significantly different niche than the adults (Haug, 2020). In the case of a complicated ontogeny, the ecological niche of the species may consist of two disparate parts of the ecospace (Body et al., 2015). Some species even have more than a single distinct larval phase, possibly occupying three or more distinct regions of the ecological space (resulting in a similar space occupation as in the polymorphism example, Figure 2).

Following these considerations, we again assume two different communities, each with five species, all of them

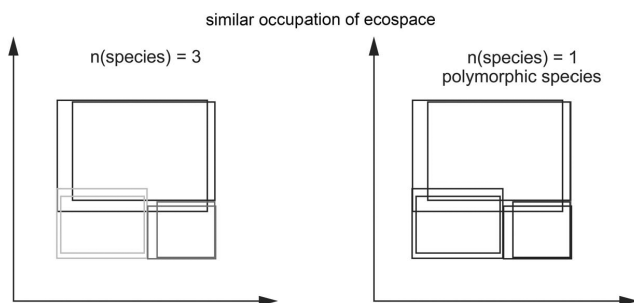


FIGURE 3 Similar ecospace occupied by three species (left) or by one polymorphic species (right).

equally abundant. If in the first community only species without distinct larvae are present, while in the second one, all species develop through a distinct larval phase, the second community would be ecologically more diverse, that is, occupy more ecological space (Figure 4). Such differences cannot be identified based on common diversity indices.

While in many approaches the focus lays on 'adult only', in fact often 'adult males only', other life stages can be used as well; still these seem largely focused on a single stage (Merritt & Cummins, 1996; Müller et al., 2013). Such approaches can hence obscure potential environmental disturbance signals affecting only single life stages (Hering et al., 2004).

2.5 | Niche distance and niche position problem

Another basic assumption in diversity indices is that not only all entities are of the same size, but also that they have the same distance or spacing between them. Yet, if we understand the niches of species as occupied areas in the ecospace, this does not necessarily have to be the case (and most often it is not).

We again assume two different communities with five species, each species occupying a similar niche size, that is, area within the ecospace, but the two communities can still differ in the distance between these areas. In such a case, the overall occupied ecospace is rather similar, but not exactly the same (Figure 5). The exact configuration of the ecospace is important since it would be reflected in the ecosystem functions and services performed by the community. Basically, the difference is the 'space in between' or 'negative ecospace'.

While the factually covered area is identical, the range is slightly larger in a case in which the distances between the individual areas are larger. In this case, the difference appears more subtle, but in cases where there are not only five species but hundreds, this subtle difference may sum

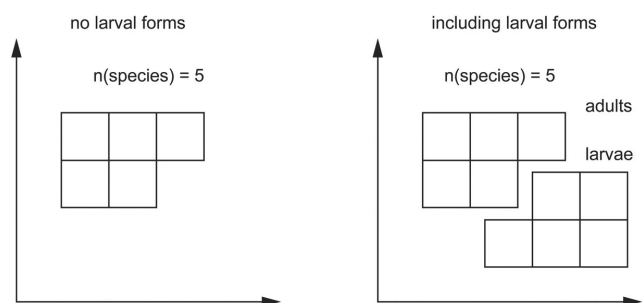


FIGURE 4 Including larval forms expands the occupied ecospace (right) in comparison to species without larvae (left).

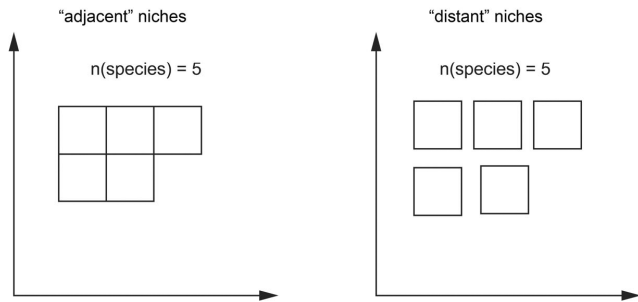


FIGURE 5 Niche position problem 1: relative position to each other. Even with the same number of species each occupying the same area, a community can have a larger ‘negative space’ when the relative positions are further apart (right) instead of being closer together (left).

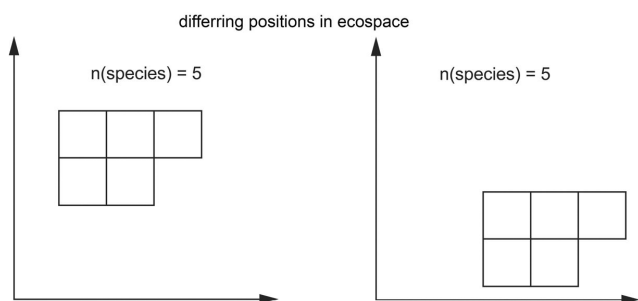


FIGURE 6 Niche position problem 2: absolute position in ecospace. Even if not only the occupied space, but also the negative ecospace (= ‘space in between’ the species) is identical, the position of two communities may well differ.

up to a significant difference in the occupied range within the ecospace.

Part of the example refers also to a different positioning of the individual areas within the ecospace, which can again create disparities. In two different communities, we may have five species each, all with similar niche sizes (area within the ecospace) that are all similarly spaced (touching each other in our example), that is, they do not differ in distance. Yet, they may still differ by simply being positioned in completely different areas of the ecospace (Figure 6).

2.6 | The problem of cryptic species

With the advent of molecular-based species delineation (or delimitation), numerous so-called ‘cryptic species’ have emerged in recent years (e.g. Bickford et al., 2007; Rehman et al., 2021). This phenomenon leads to an increase in the values measured by diversity indices. Yet, we need to ask: What does the identification of cryptic species actually mean for a community?

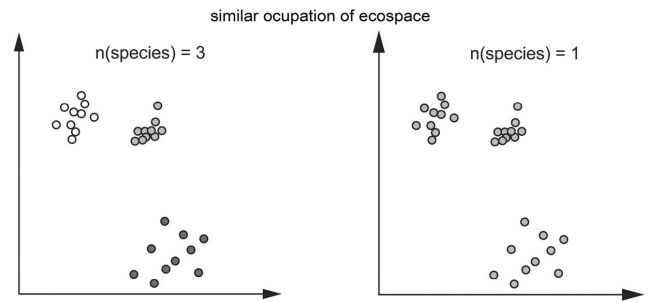


FIGURE 7 The recognition of cryptic species does not change the occupied ecospace. While there are three recognised species in one community (left), and one in the other (right), in both scenarios exactly the same space is occupied.

The answer is: possibly not that much. If species are truly cryptic, they occupy the same ecological niche (Figure 7). It is, however, increasingly clear that the term ‘cryptic species’ often simply means a species indistinguishable from another one, based on conventionally used morphological characters. Interestingly, the opposite can be true as well: Two seemingly morphologically distinct species may turn out to be a single species genetically (Lee et al., 2020). Such cases of pronounced differences (e.g. due to phenotypic plasticity) can result in different ecological functions of the two different morphotypes, leading to species with very broad realised niches (Miner et al., 2005). But also ‘cryptic’ species often become morphologically distinguishable later, as more specimens of the ‘cryptic’ and ‘initial’ species are compared and diagnostic morphological characters are identified. Therefore, many ‘cryptic’ species are presumably also ecologically distinct from the species with which they were originally lumped.

However, assuming that some cryptic species are occupying the same ecological niche, one question arises: Is a community in which the same niche is occupied by numerous species ecologically more diverse and ‘valuable’ from an ecological function standpoint? Common diversity indices would indicate so.

In principle, many discussions about cryptic species relate to a rank-height problem (see also next section). A discrete entity that had previously been recognised, for example, as a population may now be recognised as a species. Thus, the entire problem may indeed be a matter of recognition (see, e.g. Scholtz, 2014). Whether it also relates to a difference in ecological impact remains to be seen.

Despite these conceptual uncertainties, this discussion has a direct bearing on the conservation policies and practices. The case of the giant Chinese salamander (*Andrias davidianus*-complex) is a good example of this impact. The salamander was originally considered a single species but was later re-interpreted as a complex of five cryptic

species (Yan et al., 2018). Similar cases have been made for other large animals such as giraffes (e.g. Coimbra et al., 2021 and references therein). In all such cases, the split-up into several species has led to some of the new species being considered endangered and becoming protected subsequently.

In the end, the problem comes down to the old question: what is a species? Even if a formulated concept is available, the question can be expanded to how such a species can be practically recognised (Haug & Haug, 2017). This practical recognition is especially problematic as most species concepts lack a well-formulated frame of recognising species over longer time spans (Haug & Haug, 2017). Yet, exactly this aspect is crucial for any monitoring approach.

2.7 | Further rank-related aspects

So far, we have talked about species. However, diversity indices have also been applied to higher ranks (genus, family, order, etc.). This application seems to occur especially in palaeontological studies (e.g. Collins et al., 2018; He et al., 2018; Shackell & Frank, 2000), but can also be found in studies of extant organisms (e.g. Baldrighi et al., 2017; Malviya et al., 2016; Müller et al., 2013; van Klink et al., 2020).

It is noteworthy, that many ecological studies are mixing supra-specific groups of different ranks in the same analysis (e.g. Baranov et al., 2017; Müller et al., 2013). Hence even these approaches seem aware that rank height is not comparable in different lineages. The used ranks seem dependent on taxonomic expertise and available equipment required for identification, or simply on traditions existing in regional groups of experts dealing with ecosystem biomonitoring. In Germany for example, it is a tradition to generally ignore the species richness and ecological diversity of non-biting midges (Chironomidae) in the course of routine biomonitoring studies, despite their tremendous functional and structural importance and diversity in freshwater communities (Armitage et al., 1995; Sundermann et al., 2008). Without any scientific rationale, they are lumped into a single category 'Chironomidae' (e.g. single ID code in the AQEM software package commonly used in biomonitoring data assessment in Germany; Hering et al., 2004). This leads to a widely inaccurate assessment of the ecological status and ecosystem functions of the communities sampled (Orendt, 2018). Other countries such as Finland and some states of the USA have successfully integrated a more differentiated determination of non-biting midges into their monitoring approaches (Orendt, 2018; Orendt & Spies, 2012).

The principal problem of applying diversity indices to higher ranks arises from problems of ranks themselves.

Ranks lack any scientific basis, as there are no objective criteria for deciding in which case which rank should be applied (e.g. Avise & Liu, 2011; Baranov et al., 2019; Baranov, Wang, et al., 2020; Bertrand et al., 2006; de Queiroz & Donoghue, 1988; Ereshefsky, 2002; Griffiths, 1976; Haug, Baranov, et al., 2020; Hennig, 1969; Lee, 2003; Mayr, 1942 p. 291, line 3; Minelli, 2000; Müller et al., 2013; Zachos, 2011). It is evident that this notion is not new either, there is a body of literature discussing the issue of incomparability of higher ranks (Minelli, 2000; Schaefer, 1976). Therefore, diversity indices applied to higher ranks seem mostly to be a reflection of the taxonomic practice. For example, the comparison of different communities through time may tell us whether taxonomists working in a specific geological age tend to be splitters or lumpers (Burkhardt & Smith, 1990; Endersby, 2009). Both habits heavily influence the indices that will be calculated. With this sensitivity for decisions of experts, which are not necessarily reproducible, common diversity indices are a weak tool for time-related approaches.

2.8 | Non-taxonomy-related questions

As pointed out further above, larvae may occupy very different ecological niches, that is, areas of the ecospace than their corresponding adults. This niche differentiation may be one important point for the evolutionary success of species with larvae as it ensures that the different conspecific life phases avoid exploitation competition (Ayala, 1970; De Beer, 1958; Ebenman, 1992; Pechenik, 1999; Werner & Gilliam, 1984).

It seems to be generally assumed that adult morphology is more diverse than the morphology of larvae (e.g. Høeg & Møller, 2006). Yet, as already De Beer (1958) has pointed out, there are cases in which larval morphology within a certain group is quite high, while the adults are comparably uniform (see also Yamaguchi et al., 2000). Such differences may be important for conservation biology for recognising the life stages (or phases) with the highest impact on a community. Common diversity indices cannot be applied here as these are taxonomy-sensitive, making them insensitive when the compared groups represent the same taxonomic entity at different points within their life history.

This is only one example that should point out that not all diversity-related questions are taxonomy-related. Especially life history-related questions may prove to be important here. It is worth noting that in some fields of biomonitoring, such as river quality assessment, larvae are historically taking precedence before adults in the calculation of some of the diversity metrics (Merritt & Cummins, 1996), while this seems uncommon in other approaches.

2.9 | Summary of the weaknesses of common taxonomy-centred approaches

We can shortly summarise the shortcomings of common diversity indices. They are related to the fact that they:

- are only sensitive for taxonomic properties of a community, not for ecological properties of its components; factually species number is used here as a proxy for ecology;
- ignore width, distance and position of niches and ecological 'negative space', or ecological impact of key species;
- ignore polymorphic species or species with distinct larvae;
- inflate ecosystem importance of species with almost identical niches (i.e. cryptic species);
- are sensitive to rank-correlated problems (including cryptic species);
- are sensitive to the taxonomic expertise distribution and therefore are often subjective.

3 | EXAMPLE 2, A TRAIT-CENTRED APPROACH: THE 'CUBE-ECOSPACE'

3.1 | A trait-only concept

The term 'ecospace' has so far been used for different purposes. Above we have used it as a principle description of a multi-dimensional space with each dimension representing the range of a specific ecological property. The question remains how such an ecospace for a specific community can be more directly recognised. As pointed out above, diversity indices appear to proxy this space by the number of present species.

Bambach et al. (2007) have outlined an approach to compare communities through time, based on their ecological components. This approach is different from taxonomy-based indices as it is not based on the taxonomic properties, but purely on ecological properties.

Practically, each organism is classified in such an approach according to distinct properties of the organism, for example, concerning its locomotory characteristics or its feeding style (e.g. Bambach et al., 2007; Ghodrati Shojaei et al., 2015; Hajjalzadeh et al., 2020; Lam-Gordillo et al., 2021). In the traditional approach, there are three dimensions (locomotion, feeding, habitat) with six different states each, resulting in a cube composed of 216 smaller cubes. Each cube more or less equals an ecological guild. A comparison between different communities can then be based on comparing which cubes are filled and which

ones are empty and furthermore which cubes are filled to which amount, that is, which percentage of organisms in a community is in which category (= cube). The first aspect, the number of filled cubes, roughly equals diversity indices that emphasise species richness. The second aspect roughly equals diversity indices that emphasise species evenness.

So far, this approach to outline an ecospace of a community appears to have been mainly applied to palaeontological questions, but rarely to modern communities (e.g. Bambach et al., 2007; Mondal & Harries, 2016; Novack-Gottshall, 2007). While this approach can overcome certain shortcomings of the taxonomy-related indices, it itself suffers from severe limitations outlined in the following.

3.2 | Size and distance

Similar to the traditional diversity indices, a cubic ecospace is strongly simplifying complex multi-dimensional ecospace into 216 discrete units. As outlined above, discrete units implicate a similarity of each unit concerning the size of each unit and distance between adjacent units. Unlike the diversity indices, there is a certain level of reproducibility and quantitative characterisation of the position within the space. Hence, communities with an identical number of filled cubes (and equally filled cubes) can still be recognised as different based on which cubes are filled (e.g. an upper row of five cubes vs. a lower row of five cubes).

Still, it must be clearly recognised that a complex multi-dimensional ecospace is proxied in this case by a rather simple three-dimensional space that uses sizes and distances of cubes that are unlikely to reflect the true sizes of areas in the ecospace and distances between them. This does not seem to be a significant improvement when compared to common diversity indices.

3.3 | Classification

As it was applied by Bambach et al. (2007), the cube-ecospace approach is based entirely on a classification of the different organisms within a community into discrete categories. Hence, the concept heavily relies on the quality of the primary classification, suffering from the same subjective problems as trait assignments to the supra-specific groups.

As discussed above for species and ranks, classification can be difficult or at least challenging. It needs to be based on reliable criteria, which allow other researchers to come to the same (or at least largely comparable)

conclusions. Therefore, comparing communities with such an approach may end up in comparing the quality (or practice) of the classification of the organisms into discrete classes.

3.4 | Reproducibility

Bambach et al. (2007) have specifically designed their approach for comparing different communities through time. Therefore, it is designed specifically to be applied to fossil communities. Yet, some (if not many) of their categories cannot be directly observed in a fossil but have to be inferred to a certain degree from comparison with living relatives. While one could argue that this is a specific problem of studying fossils, it also applies to a considerable number of modern organisms. Our capabilities to observe organisms living in hard-to-access habitats, for example, in the deep sea or the interstitial hyporheos are still very limited. Hence, also here certain aspects of their ecology need to be inferred (e.g. Drazen & Sutton, 2017) based on the observed morphologies. Even common freshwater species used in biomonitoring are relatively difficult to observe at different life stages, which leads to extrapolation of the data from their morphology or better-studied-related species (Cranston, 1990).

The difficulty of such estimations is that different researchers will come to different conclusions. Hence, the reproducibility of the classification into Bambachian cube categories is not always given.

3.5 | Coarseness

As applied by Bambach and colleagues, the entire scheme of ecological classification remains rather coarse or 'pixelated'. While it may be sufficient for recognising differences in certain communities through time, it seems to be too coarse to recognise differences in modern communities. We can also expect to recognise a difference between desert communities and rainforest communities, but can we expect to find differences between different rainforest communities?

This coarseness is partly related to the classification problem. If we were able to capture finer differences in the community structure, we would be able to gain a finer resolution.

This aspect also comes back to another problem, namely a priori assumptions of the states and traits of an ecosystem that have to be made to create such an ecospace. These are, of course, limited to our knowledge about the organisms, which is mostly not an issue for a wet meadow, but clearly one for the deep sea.

3.6 | Dealing with polymorphism

The cube-ecospace also has difficulties in dealing with polymorphic forms and especially with differences between larvae and adults. While most representatives of Reptantia (Eucrustacea), Eleutherozoa (Echinodermata) and Mollusca are benthic as adults, many of them are planktic during their larval life (Pechenik, 1999).

In principle, this difference in life habits could be simply coded as a single species occupying two of the cubes. However, concerning fossil communities we face the challenge of taphonomic bias as certain life habits as well as certain life stages are more likely preserved than others.

Can we infer the presence of the larvae based on the presence of certain adults? Most likely not. Larvae may live in quite different habitats than corresponding adults. Also, larvae and adults do not necessarily evolve at the same speed (e.g. Klingenberg, 1998; McNamara, 1986). Certain adult forms may have already evolved and not yet possessed the highly specialised larvae known from modern forms (Haug, Audo, et al., 2015) or vice versa (Haug, Martin, & Haug, 2015). Hence, although the cube-ecospace could in principle deal better with the polymorphism, the practical application is also quite challenging.

3.7 | Summary of the weaknesses of the trait-centred approach

We can shortly summarise the shortcomings of the cube-ecospace. They are related to the fact that it:

- ignores width, distance and position of niches and ecological 'negative space', or ecological impact of key species;
- ignores polymorphic species or species with distinct larvae;
- is sensitive to the quality of the initial classification.

4 | EXAMPLE 3, COMBINED TAXONOMY-TRAIT APPROACH: FRESHWATER BIOMONITORING

4.1 | Taxonomy and traits combined

The German saprobic index focuses on a correspondence between the quality of the environment and taxonomic composition of a community. It was pioneered by Kolkwitz and Marsson (1902) and remained conceptually unchanged ever since. The base assumption is, that different species occupy different habitats and have different levels of tolerance of environmental factors (Kolkwitz

& Marsson, 1902; Merritt & Cummins, 1996). Knowing these traits of the species should facilitate making complex inferences on the environmental conditions, based on the taxonomic composition of the communities.

Applying this approach to freshwater monitoring (e.g. Brown et al., 2007) has one severe problem, leading to further challenges: the knowledge of the biology of many indicator species is incomplete (Merritt & Cummins, 1996), despite 200 years of study of freshwater-inhabiting forms. Looking at the freshwater ecology database (<https://www.freshwaterecology.info>)—the chief source of data on ecological traits—reveals this quite drastically: There are 323 species of caddisflies (Trichoptera) in Germany. Of these, 87% of trait state cells are empty, that is, the traits are unknown. For 127 species of stoneflies (Plecoptera) in Germany, there are 91% empty cells, for 142 species of mayflies (Ephemeroptera) 93% empty cells, for 117 species of freshwater (non-insectan) crustaceans 98% empty cells and finally for 73 species of true bugs (Heteroptera) 99% empty cells.

While one can argue that some of these trait states are redundant data, which are partially overlapping with each other, the state of our knowledge of the ecology of common indicator species in one of the best-studied countries in the world is simply poor (Baranov, Jourdan, et al., 2020). It has been demonstrated empirically with a concept of ‘taxonomic sufficiency’ that decreasing resolution of identification leads to a poor fit between environmental monitoring and the functional state of communities (Beermann et al., 2018; Müller et al., 2013).

4.2 | The structural problem of too much work for too few experts

Missing knowledge of the biological aspects of so many species led authors to interpolate the traits from their better-studied relatives (Jähnig et al., 2021). Hence, many current monitoring schemes reconstructing the functional aspects of communities based on trait space are operating on the assumption that entire groups of species, genera or even families do occupy similar niches (Hering et al., 2018). While such an approach may have certain merits, it also has the potential to lead to severe errors in biomonitoring, as even closely related species can have vastly different traits (Bouchard et al., 2005; Cranston, 1990; Prat & García-Roger, 2018). An ideal solution to this problem would be more research on the ecology and biological traits of indicator organisms, but such studies are time-consuming and expensive.

In addition, there is, nowadays, a structural problem: The advent of biomedical research in the second half of the 20th century together with a changing mode and

priorities in funding basic research has led to a steady decline in the number of professionals dealing with the field of organismic biology (Daglio & Dawson, 2019). Universities have experienced a steady decline of chairs and courses dedicated to the field of organismic biology and all its sub-disciplines. Similarly, the number of zoological and botanical curators in museums and comparable institutions has declined significantly (by 10% in Australia and New Zealand in 25 years; Taxonomy Decadal Plan Working Group, 2018). On the backdrop of the declining number of the experts in organismic biology, the number of challenges requiring this very expertise has significantly increased.

The continuing deterioration of the biosphere has led to an increasing pace of the extinction of species. The rate of the new extinction event is so prominent against common background levels that many people already talk about the ‘Sixth Great Extinction’ (Cowie et al., 2022; Dirzo et al., 2014). The expertise of fewer organismic biologists becomes stretched across more fields (Hutchings, 2020) leading to the ‘taxonomic impediment’—a growing gap between the societal need for organismic biologists and their number.

This leads not only to a severe backlog of work in organismic biology, but also to a decreased amount of training for a new generation of organismic biologists. As the biomonitoring approach discussed here relies on trained organismic biologists able to reliably identify organisms (Carvalho et al., 2005; Collen et al., 2008; Engel et al., 2021), the ‘taxonomic impediment’ has a direct impact on it.

As a result of the lack of sufficient organismic biologists, identifying organisms in surveys mostly relies on so-called ‘parataxonomists’. A ‘parataxonomist’ is a person involved in biodiversity studies with a lower-level training than an organismic biologist, but can assist in studies via labour division (Krell, 2004). Originally, they were tasked with specimen collecting and cataloguing in large projects to free up trained organismic biologists for specimen identification. Information in biodiversity studies was supposed to flow from parataxonomists collecting specimens to organismic biologists identifying them to ecologists using the collected data to make conclusions about the ecosystems (Ward & Stanley, 2004).

Nowadays, information often flows from a parataxonomist directly to an ecologist, and, in principle, that can work well enough. In worse cases, all three tasks are combined into a single person, as most of the research and monitoring institutions conducting surveys of biodiversity are permanently understaffed. Practically, lab technicians and students often perform the identifications, while lacking a proper in-depth training to do so. Additionally, most of the monitoring laboratories are dealing with a

huge number of samples and have only a limited qualified workforce available. That situation can lead to fatigue and cause mistakes in identification. This in turn leads to the proliferation of identification errors, which again lead to errors in the assessment of the ecosystem status, which finally leads to faulty decision-making down the line. In consequence, specimens are often not identified to species level, but to supra-specific groups (see discussions above). Automated approaches (Wührl et al., 2022) have the potential to at least partly improve this situation but are still at their infancy.

4.3 | Summary of the weaknesses of freshwater biomonitoring

We can shortly summarise the shortcomings of freshwater biomonitoring:

- Determining species is time-consuming, and too few people are available for this task.
- Reliably assigning traits to species is factually not possible due to a severe knowledge gap.
- Assigning traits to supra-specific groups is basically meaningless.

Basically, as a combined taxonomy-trait approach, this one suffers from similar problems as taxonomy-only and trait-only approaches.

5 | COMPARISON OF THE COMMON APPROACHES

Despite these outlined limitations, ecospace approaches, as the one proposed by Bambach et al. (2007), have the advantage, compared to diversity indices, of not being dependent on arbitrary taxonomic ranks, from which combined taxonomy-trait approaches suffer as well. Trait-only approaches are also superior in not relating to the structural properties of the community, but actually involve functional properties, as do taxonomy-trait approaches. Still, due to the constraints of the habits of ‘assigning traits’, both approaches share problems with common taxonomy-only approaches: all are strongly sensitive to the quality of the input data, which are factually decision-dependent.

This problem relates to the fact that all three examples measure discrete entities (guilds and taxonomic units respectively). The quality of these approaches is therefore strongly dependent on the quality of the grouping of the discrete entities. As pointed out above, this sorting is currently largely arbitrary for species (even more so for

supra-specific groups), but also for ecological entities such as guilds (which often remain rather coarse).

Another weakness shared by these approaches is that all recognised entities are treated as if they would have an equal weight in the system. They are treated as if they would be equal in ‘size’ (niche size, guild size) and ecological impact, but also equally different, that is, in an equal distance in the real ecospace.

Assuming that all guilds have the same weight in the community is an oversimplification. The functional and structural distance between some guilds may be large, while others may be closer to each other. This again relates to the problem of recognition. For some areas of the ecological space, it may be easier to differentiate between different guilds. In such a case, the resolution of our structural models will be higher compared to the areas of the ecological space, where it is more difficult to provide minute subdivisions.

These considerations point out that a different type of measure for comparing the ecological properties of two communities (and comparable approaches) could, or better should be a non-discrete-ecospace approach. In the following part of this communication, we discuss possible advantages of such an approach. We furthermore will attempt to outline how such an approach could be practically applied.

6 | A POSSIBLE WAY: A NON-DISCRETE ECOSPACE

6.1 | A non-discrete-ecospace approach and its possible advantages

We are proposing the term ‘continuous’ or ‘non-discrete’ ecospace to denote an approach for ecospace construction, which does not involve arbitrarily classified discrete units as its basis. Hence, it would not depend on assigning (largely unknown) ecological traits to higher ranked groups.

Such an approach would also be generally independent from taxonomic rank problems. It would, therefore, not depend on the recognition (or lack of recognition) of cryptic species or the ‘correct’ identification of family vs. sub-family (short note: there can be no ‘correct’ in this discussion). Also, comparisons of communities through time, that is, palaeo-communities, which are currently often represented by simple lists of the supra-specific taxonomic units, would be less prone to artefacts. Compared to cube-ecospace approaches, a continuous, non-discrete one would not suffer from the coarseness of too few recognised niches. It would also not depend on the quality of niche recognition.

The core challenge remains now how such a continuous ecospace could look like. Moreover, we need to outline how such an approach can be practically applied.

6.2 | Towards a non-discrete ecospace approach

How could we practically design a non-discrete ecospace approach? The ecospace of an individual species should be a reliable proxy of the ecological niche of the species. We know that ecological niches are in principal certain areas within a multi-dimensional ecospace. Inferring all these dimensions for a single species is practically impossible. So, how can we expect to be able to do this for an entire community? We simply cannot. Hence, we need to use strategies already established for more traditional approaches of diversity and conservation biology research.

6.3 | Entire samples or proxy groups

Depending on the exact question behind the comparison, it can be feasible to simply take entire communities represented in a sample into account. For others, it can be necessary to restrict such a comparison to a specific, well-delineated systematic group, or several of these, but these should not be limited to a specific taxonomic rank. Instead, such well-delineated groups should be monophyletic. Well-delineated usually means a comparably long evolutionary branch (a group with a characteristic morphotype, normally as earlier derivatives of this lineage went extinct and at best have not left fossils of their early lineage); hence the recognition of 'the lower end' of such a proxy group should not be problematic. Still, for comparison through time such delineations may be more difficult and should thus at best be correlated to apomorphy-based monophyletic groups.

While it may appear that in this case, taxonomy would still play an important role, the use of an apomorphy-based 'threshold' is not a matter of taxonomy, but of phylogenetic systematics. Such an approach would be less depending on decisions and should be reliably repeatable.

What groups could be used here? This decision would partly depend on the focus of the study. For comparing entire communities, species-rich groups with a possible broad impact would be good candidates. Possible candidates from Euarthropoda (which are generally considered ecologically important) for terrestrial communities could be beetles (Coleoptera), or an ingroup of it, or true bugs (Heteroptera). For freshwater, water fleas (Cladocera) or

mosquitoes in the strict sense (Culicidae) could be good representatives. For other questions, these groups may be less informative. In any case, the practice to choose proxy groups for comparing communities seems to be an already well-established practice in common diversity comparisons (e.g. Bonada et al., 2006; Mellin et al., 2011; Tyler & Kowalewski, 2017).

6.4 | Morphospace as a proxy

Diversity measures involve either taxonomic properties of a community (examples 1 and 3 from above) and/or assigned traits (examples 2 and 3) as a proxy for the ecological diversity of a community. These taxonomic or assigned-trait properties are practically not directly observed, but usually are identified on morphological properties of an organism.

To come back to example 3: in freshwater communities, the interactions of organisms with currents and buoyancy are one of the main drivers of the morphological evolution of aquatic animals. Freshwater animals have developed a range of body shapes to adapt to the range of hydrological conditions, temperatures and feeding modes. Hence, their shape is directly coupled to ecological properties. When specialists assess the ecosystem status using the taxonomic diversity of organisms, they make a double inference. As outlined above, first they infer the taxonomic position of the organism, then they, however, equivocally infer which ecological traits should be associated with this organism.

Although the genetic species concept has started to change this two-step inference (Baloğlu et al., 2018), most species known so far are not based on differences in genes or on actual recognition of reproduction boundaries out in the field. Instead, morphology is the most commonly used method to recognise species as such initially. Furthermore, when inferring the diversity of a certain community, usually morphology is used to determine specimens as representatives of a specific species. For fossil communities, this is, of course, the only possible way.

We are proposing to approach the construction of morphospaces from the principles of morphometry by using methods to capture the simplified shape of organisms, by measurements, landmarks or outlines (Cameron & Cook, 1989; Guillerme et al., 2020). Since shape is a reflection of function, documenting shapes of organisms in the community is capable of representing functional diversity in the studied system (Baumiller et al., 2010).

The advantage of directly using the morphospace as a proxy is that the decision-making process of interpreting

morphologies into discrete units (species, traits) is eliminated. If used as a proxy for ecospace, the morphospace consequentially becomes a morpho-ecospace. It is also possible to additionally augment morpho-ecospaces with measured ecological traits (temperature, salinity, etc.), at least in extant communities.

6.5 | Ecologically important structures

Morphometry can be applied to entire body shapes (e.g. Baranov, Wang, et al., 2020; Haug, Baranov, Wizen, et al., 2021; Haug, Haug, & Haug, 2021). But in many cases, individual structures of the body are better to be considered, for example when certain body parts are stiffer and less prone to distortion. In such cases, the morphospace used as a proxy for ecospace should involve properties of morphological structures that are of ecological meaning. Genitalia structures are often used in taxonomic approaches to differentiate species, therefore interestingly influencing diversity indices. Yet, these structures seem less important for a morpho-ecospace as they have little to no influence on the ecosystem functions of an organism. Properties describing the overall body organisation, locomotion (or anchoring) structures, feeding apparatus and alike seem to be most important. In principle, these are also morphological structures that would be important for the cube-ecospace approach.

6.6 | Quantifying, not ‘qualifying’

The cube-ecospace approach and the diversity indices are discrete. Many morphospaces are discrete as well, using, for example, absence or presence of certain characters. All these approaches are quantitative in a way that they count or measure certain properties. However, the entities counted or measured have been categorised before. This categorisation is not quantitative, but qualitative.

As pointed out, we aim at using a non-discrete approach. Hence, the morphospace used as a proxy for the ecospace should be a continuous one. Morphological characters used in such a morphospace should be plastic (measured) and not meristic (counted). In principle, simple length, area and volume measurements could be appropriate. Yet, more complex properties such as shape have even more potential.

Measurements should be used as standardised denominated values to get rid of the absolute size-difference effects. Also, real size of the organisms might be recorded and later applied, as it may reveal distinct

size differences between certain communities (Baranov et al., 2022).

6.7 | Morphospace diversity approaches so far

In ecology, morphospace analyses have so far only been used sparsely and almost never to study the shifts in the ecological properties in a community. For example, Lombarte et al. (2012) have dealt with shifts in fish morphospace after disturbance in a river, showing that the ‘Ecomorphological Diversity Index’ (EMI), a measure of the morphological complexity of the community, was decreasing in response to a disturbance (in their case removal of macrophytes). Likewise, Pausas and Verdú (2008) have shown that disturbance from fires is causing a reduction in the morphospace occupancy by terrestrial plants. Heller (1987) and Cameron and Cook (1989) used the shape and size of land snail shells to predict habitat use. For comparing the diversity of fossil larvae to their extant counterparts in various lineages of Insecta, we and colleagues have used shape analyses, successfully identifying changes in diversity through time (e.g. Baranov, Wang, et al., 2020; Haug et al., 2023; Haug, Baranov, Wizen, et al., 2021; Haug, Haug, et al., 2020, 2022; Haug, Haug, & Haug, 2021; Haug, Haug, Zippel, et al., 2021; Haug, Posada Zuluaga, et al., 2022).

6.8 | Disadvantages of the suggested approach

The suggested approach has certain disadvantages common for methods of community assessment methods (Navarro et al., 2004) that are all related to the elimination of classification. Classifying a single individual may be very simple and comparably fast. A short look can in some cases already allow the identification of a specimen to a certain species or a guild. The suggested approach demands instead that each specimen is, for example, measured at numerous dimensions, landmarks are set or outlines of certain structures are registered. It, therefore, will take more time to record the same number of individuals for a specific community. This disadvantage will be immediately balanced by the larger amount of data recorded for each specimen and even more by the advantages discussed in the following. Moreover, such data may potentially be gathered with automated set-ups.

Furthermore, this approach, like most other assessments, is dependent on which sampling protocols are

applied. Organisms still have to be caught, and the manner of which dictates which organisms can be obtained. Sampling protocols should be therefore carefully considered. The time of day and year for sampling is also important, as morphologies within a community are not expressed equally all year round, larvae and adults of the same species often peak at different points in time.

6.9 | Advantages of the suggested approach

In the outlined approach, not a species or a guild is registered, but each individual is plotted into the morpho-ecospace. This approach will therefore reflect variation within a species or guild much better.

As the approach is less dependent on decision-making, identification errors by non-specialists will not influence the results. This aspect makes such an approach attractive also for citizen science projects. Ultimately, the suggested approach even has the potential to become automated.

A morpho-ecospace approach might circumvent the taxonomic gap and lack of workforce limiting morphological identification as well as material and equipment costs required for DNA barcoding. Collection and measurements could be done quite cheaply. Even specimens that cannot be properly identified to a species or guild can be included. Fossil specimens that are not well preserved with taxonomically important features can be included, if the structures to be measured/analysed are preserved. In this way, it is possible to make use of fossils that are often considered of low value for such studies.

Larvae and other immatures that can often not be easily identified to species, in samples of fossil and extant species, can be included without problems. Larvae will most likely plot in other areas of the morpho-ecospace than their corresponding adults, with this reflecting the ecological differences. Larvae and adults of a certain group can even be compared for their morpho-ecological diversity, a possibility not provided by most current approaches.

While taxonomic identification is not a prerequisite, there is no harm in identifying specimens to a certain taxonomic level. The morpho-ecospace can, therefore, well be combined with taxonomic or phylogenetic questions and approaches.

6.10 | Trait diversity

The limits of taxonomy-based diversity indices (such as the Simpson or the Shannon Index) have been recognised by numerous researchers in the past (e.g. Clarke & Warwick, 2001; Desrochers & Anand, 2004; Schweiger

et al., 2008). In recent years, they have therefore been amended by ‘trait diversity’ approaches or functional diversity indices (Díaz & Cabido, 2001; Menezes et al., 2010; Schleuter et al., 2010; Villéger et al., 2008). So far, trait diversity seems to be a kind of umbrella concept uniting different types of data, including, for example, aspects of the morphology, food composition or preferred ecological factors (Mason et al., 2003; Schleuter et al., 2010). Some of these data are measured in non-discrete dimensions, others seem to depend on a priori classifications. This inconsistency demonstrates that trait diversity is so far no uniform concept, but a loose collection of different concepts. How does it relate to the here outlined approach?

The morpho-ecospace approach could well be understood as a type of trait diversity, but an explicitly non-discrete one. As pointed out above, it is in principle unproblematic to amend the morpho-ecospace by true ecological axes, such as the preferred temperature of activity, time of activity or preferred salinity.

7 | CONCLUSIONS

In summary, the here outlined morpho-ecospace approach has the following advantages over taxonomy-centred, trait-centred or combined approaches:

- The decision-making is reduced, hence it is less dependent on the quality of the initial classification.
- It directly uses morphology as a basis, while in other approaches morphology is also used as the basis, but first interpreted; hence, the level of inference is reduced.
- Aspects usually not considered, such as ontogeny or polymorphism, can be incorporated.
- There is no dependence on arbitrary entities such as species, which lack proper time boundaries, hence all time-correlated comparisons, including fossils, can be performed.
- Specimens that cannot be classified in other approaches can be included.
- The approach can be combined with already established ones.

AUTHOR CONTRIBUTIONS

Conceptualisation: Joachim T. Haug, Carolin Haug; methodology: Joachim T. Haug, Viktor Baranov, Florian Braig, Carolin Haug; formal analysis and investigation: Joachim T. Haug, Viktor Baranov, Florian Braig, Carolin Haug; writing—original draft preparation: Joachim T. Haug, Viktor Baranov, Florian Braig, Carolin Haug; writing—review and editing: Joachim T. Haug, Viktor Baranov, Florian Braig, Carolin Haug; funding acquisition: Joachim T. Haug.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no competing interests.

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