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Research Article

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Are species largely redundant? Testing the reliability of increasingly complex trait-based classifications in understanding Canadian Arctic ecosystems

Abstract

Background: In recent years, some ecologists have advocated the use of functional groups instead of direct species in linking site composition to the environment. They could potentially reveal connections between distant sites and aid in the formation of widely-applicable environmental policies. Several studies have compared the efficiency of using functional groups, in which species are grouped based on functional traits, like feeding method or size, to using species directly. However, few have looked at the effect of varying the complexity of functional groups when compared to species data. This study compares functional group classes of varying complexity, with complexity defined as the number of traits considered, to species data. The hypothesis that more complex functional group classes, compared to less complex classes, tend to approach the results obtained when using taxonomy, is tested.

Methods: In testing this hypothesis, this study uses site composition data from aquatic floor (benthic) ecosystems in the Canadian Arctic. Four functional traits were considered important to describe these species: Bioturbation (sediment disturbance), body size, feeding habit and mobility. These traits were used to segregate species into functional groups of varying complexity, with complexity level determined by the number of traits (out of four) being used. Four environmental characteristics were considered for each site: Chlorophyll a, phaeopigments, depth and salinity. In order to test how similar functional group data is to species data, we sought to determine whether the same environmental variables were important in explaining site composition. This was determined by BIO-ENV analyses and Spearman Rank correlations. Mantel permutation tests then determined whether the correlations were significant.

Results: While all levels of complexity, from one to four functional traits, showed some significant correlations (Spearman Rank ≥ 0.5 , $p \leq 0.05$) between site composition and environmental variables, there was no general trend suggesting functional group complexity correlates with greater similarity to taxonomic data. For presence/absence data, all functional results, regardless of complexity, pinpointed only phaeopigments as important, while presence/absence species data also included chlorophyll a and depth. All results with strong and significant correlations ($r \geq 0.5$ $p \leq 0.05$), regardless of data type or complexity, maintained a measure of food supply (Chlorophyll a or phaeopigments), demonstrating its importance in determining ecosystem composition at these sites.

Limitations: Potential improvements include measuring traits directly from the organisms, considering more environmental variables and increasing the number of functional traits considered. Which traits are considered also vary with each study.

Conclusions: The hypothesis was not validated by the results. When pinpointing the most complex functional group class (the most important variable), rather than a less complex class, it was not guaranteed that the chosen variables would be the same as species data. Some classes of less complexity showed greater similarity to full species data. Some outcomes, like the presence/absence results, also imply certain species redundancies in the ecosystem, particularly regarding depth. These results have implications for the concept of functional redundancies in ecosystems, an important point in developing widely applicable environmental policies.

Introduction

Linking species compositions to environmental variables is an important concept in ecology. Some ecologists have pushed the use of functional traits, instead of taxonomic information, in relating organisms to environmental variables. Functional traits, from feeding type to size, can be used to form functional groups, with many ways of defining a functional trait (1). Some researchers define them as the traits which impact the fitness and individual performance of organisms through effects on growth, reproduction and survival (2). Others have focused on ecosystem processes

and an organism's response to environmental variables (3). The definition given by Harrington et al. (4) attempts to combine the two views by suggesting that a functional trait can both determine how an organism responds to pressures (response trait) and/or the effects the organism has on ecosystem processes (effect trait). Depending on the type of organism, functional traits can include morphological, biochemical, life-history and behavioral traits (4). Functional groups are formed by grouping species with the same functional traits together (4). For example, if the two functional traits of mobility and feeding are considered, all species that are Hemimobile Carnivores are categorized in the same functional group.

Understanding functional groups is vital in the study of redundancy in ecosystems. There are many theories regarding species redundancy. Species may be seen as unique, each offering a specific and significant effect on the ecosystem. In the “riveting” hypothesis, each species is like a rivet – remove enough and all ecosystem functions fail (6). Alternatively, many species may be redundant. Provided that there exists some species that can fill a functional role, like primary consumers or decomposers, the ecosystem functions (7). One species can replace another with the same function and fitting the same functional group. These are two extreme views, of course. Even if species are partially redundant, having redundant species can make ecosystem function more reliable and offer greater resilience to perturbation (8, 9). Understanding how closely functional information relates to species information is necessary to understand the role of redundancy.

The use of functional groups has several advantages over taxonomy. Its taxon-independent nature can harmonize data from different studies and remove linguistic confusion (10). Collecting functional data is also less costly and requires less taxonomic expertise (30). Trait-based systems can also help compare data from different locations with ecologically similar species (36). They can make ecological similarities between areas clearer than simply relying on species present (10). Functional group information about community composition is particularly helpful if many species are functionally equivalent and substitutable between sites (i.e. there is redundancy) (12).

A potential benefit of using functional groups is in the formation/management of environmental policies. Generally, environmental policies seek to be standardized and to have wide geographic application (27). Policies should also be trustworthy when considering distinct species compositions at different locations (27).

Potentially, if one could understand how species that fit into a functional group react to environmental changes (i.e. “medium size active burrowers”), wide-reaching policies could be formed. Functional traits have been used in several management fields, including in creating protected areas and detecting/predicting anthropogenic impacts. For instance, by considering trait compositions at key sites rather than only taxa, relevant Marine Protected Areas and habitat models can be developed (35, 13). Trait-based systems can also help predict the success of ecological restorations (14). Similarly, several studies have looked at using functional classifications in gauging anthropogenic stress. Several stressors, including metal leaching and eutrophication can be considered (27, 28, 29, 32). In aquatic systems, benthic invertebrate species are commonly used as ecosystem health bio-indicators and the stability of benthic communities often hinges on the pollution sensitivity of these species (30, 31). Mobility, size and feeding mode can be traits affecting pollution tolerance in benthic communities (30, 32, 25). Functional traits are also beneficial in predicting extinctions. For instance, extinction scenarios can follow clear size patterns, with larger organisms becoming extinct first (28). So, if considering body size is as valid as taxonomy, general extinction patterns could be calculated. Naturally, considering only one trait, like size or feeding, might not be as specific as taxonomy. Increasing the complexity of functional group information could potentially remedy this, and several approaches exist. For instance, Rawer-Jost et al. (32) discuss potential benefits/drawbacks of increasing levels within one category of trait (i.e. feeding) when identifying anthropogenic stressors. Others suggest combining evolutionary information and biological traits (33).

A common approach is to combine distinct categories of functional traits, including feeding, size and mobility, in segregating species into functional groups (27-29, 34). For instance, several functional traits, including feeding mode, reproductive strategy and spawning season, were combined to segregate fish species into functional groups based on stress sensitivity (29). Similarly, to understand extinction effects in coastal benthic communities, several traits including size, mobility and sediment mixing/bioturbation were used to segregate species into groups according to their impacts on ecological processes (28). In fact, the use of functional groups based on multiple traits has been shown, in certain benthic communities, to be more efficient than species abundances at indicating/identifying anthropogenic impacts (27). As Kenney et al. (30) point out, however, a remaining issue regarding functional traits in policy is the value of consid-

ering traits in combination versus individually.

While several studies have sought to compare the use of functional groups to taxonomic data, few have looked at the effects of increasing the complexity of functional groups (15-17). For the purposes of this study, complexity in functional group class is determined by how many traits are used in forming the functional groups within this class (See Table 1 and Table 2 for terminology).

There have been several studies on varying taxonomic resolution, which can be used as a template to understand why varying functional group class complexity is informative. For instance, several researchers tested whether using lower resolution taxonomic data, such as genus, family or order, is as effective as using species information (15-17).

We applied a similar conceptual model. For instance, as taxonomic categories become more detailed and approach the species level, functional group classes can become more complex as they approach the species level data. Conceptually, an order could be analogous to a simple functional group class constructed from one functional trait, whereas a genus might be similar to a more complex functional group class containing groups based on a greater number of traits. Of course, such analogies are imperfect, but help visualize the logic of increasing functional group complexity. Functional group information is more complex to work with, however, because the same level of complexity can result from different functional traits. For instance, a class that considers two traits—mobility and size—is at the same level of complexity as another that considers two traits, feeding and bioturbation, but each class considers different traits.

This study explores how the number of traits used to form functional groups (i.e. the complexity of functional group classes) affects the reliability of trait-based systems. We sought to determine whether results obtained using more complex functional group classes are closer to full species data than using less complex classes. To assess their similarity, we relied on identifying the environmental variables that are important in explaining site composition. We hypothesized that as one moves from simple to more complex functional group classes, the environmental variables pinpointed as essential should become more similar to results obtained using taxonomic data. Greater similarity is predicted in results between complex functional group classes and species data, than simple functional group classes and the same species data. For instance, if species data pinpoints only variables A, B, and C as necessary, and one of the functional group classes also pinpoints only these variables as necessary, it should be the most complex functional group class (i.e. the one that uses the greatest number of traits in grouping species).

Methods

Data Source

To test the hypothesis, a dataset of species composition at various sites, along with environmental measures, was required. Data previously collected by Link et al. (18) from Canadian Arctic marine benthic ecosystems (as part of the Canadian Healthy Oceans Network-NSERC) was used. Samples were collected from nine sites in 2008 and 2009. Several environmental variables, including chlorophyll a, phaeopigments concentrations ($\mu\text{g g}^{-1}$), depth (m) and salinity ($\mu\text{g g}^{-1}$) were recorded at each site. Taxonomic information, both diversity and abundance, was also recorded for each site by Link et al. (18). Invertebrate organisms were identified to the lowest possible taxonomic level, usually species, resulting in 311 taxa. Species predominantly fell into the Polychaeta and Malacostraca classes. See Link et al. (18) for a complete list of taxa identified. The identified taxa were also classified using four functional traits commonly considered important in benthic ecosystem processes: Feeding/diet, body size, bioturbation (sediment disturbance), and mobility (18).

We used this dataset, focusing on the year 2009, to experimentally test my hypothesis. We segregated species into functional groups based on different combinations of the four functional traits (body size, mobility, bioturbation, feeding/diet). The number of levels within each functional trait varies. Size and mobility have three levels, while bioturbation has four



(Table 1). The six feeding levels were not mutually exclusive and combinations were possible. For instance, some species were both omnivores and filter feeders. This resulted in 11 possible levels for this trait.

Functional group classes were formed for each level of complexity, ranging from Complexity 1 (considering only one functional trait) to Complexity 4 (considering all four functional traits). A total of 15 classes were formed. For instance, functional group class “Size-Feeding-Bioturbation” is a class of Complexity 3, in which the functional groups within it consider those three functional traits (See Tables 1 and 2). Three types of site composition data were considered for both functional groups and species: Raw abundance, relative abundance and presence/absence data.

Four environmental variables were considered: Chlorophyll a, phaeopigments, salinity and depth. They were chosen due to their key roles in arctic benthic ecosystems. Both chlorophyll a and phaeopigments, as components of algal biomass, are commonly used measures of food supply (24). Benthic organisms rely heavily on this biomass, which descends through the water column to the sediment floor (19). Depth is also important in determining ecosystem composition and has been shown to play a role in determining functional trait compositions in benthic ecosystems (25). Salinity is also important in the benthos, often affecting an organism's ability to survive (26). To reduce the effect of outliers, all environmental measures were log (1+x) transformed.

Category	Level
Feeding/Diet	C=Carnivorous (predator or passive suspension)
	D=Surface deposit feeder
	F=Filter/Suspension feeder
	O=Omnivorous (scavenger)
	P=Parasite
Size	S=Surface deposit feeder
	S< 3 mm
	3 mm<M<10 mm
	L>10 mm
Mobility	M=Mobile
	S=Sessile
	H=Hemimobile
Bioturbation	B=Active burrower (diffusive)
	G=Gallery burrower
	S=Surface dweller
	T=Tube burrower

Table 1. The Functional Traits considered as well as the levels within each trait

Terminology	Example
Functional Trait	eg. Mobility
Functional Trait Level	eg. Sessile
Functional Group	eg. SLD for sessile, large, surface deposit feeders
Functional Group Class	eg. "Mobility-Size-Feeding"

Table 2. The terminology used in the study and examples for each term. A Functional Group Class contains the Functional Groups formed using specific Functional Traits.

Statistical Analysis

We used a procedure similar to Heino (15), who compared results obtained with species data with that of lower taxonomic resolutions, including genus, family and order. He determined, using BIO-ENV analysis, the “best subset of environmental variables” to explain the relationship between site composition and the environmental variables for each case (15). Results were analyzed by comparing which variables were found in all levels of taxonomy and how reliable using lower resolution information can be. A similar procedure was done in this study, with the added aspect that functional group classes can be of the same complexity but be formed

using different traits.

We performed similar statistical tests to determine whether more complex functional group classes are closer to the results obtained with species data. The hypothesis predicts that the variables selected as vital in explaining the relationship between site composition and the environment, determined with BIO-ENV, will vary with functional group class complexity. The most complex class should pinpoint the same variables as those selected with species data. For the purposes of this study, the hypothesis does not prohibit a less complex class from also selecting the same variables as species data, providing the most complex functional group class does likewise. Specifically, the BIO-ENV analysis calculated Spearman Rank correlations for each functional group class to determine the best subset of environmental variables to explain the composition in the nine sites (20). Mantel permutation tests were used to determine the significance of these correlations. Functional group classes that did not give significant results ($p \leq 0.05$) were discarded and only results with correlations ≥ 0.5 were included in interpretation.

Results

The results of the BIO-ENV analysis, which determined the best subset of variables available to explain the relationship between site composition and the environment, were varied in terms of significance and correlation strength (Spearman's Rank correlation rs), although all correlations were positive (Table 3 and Table 4). Results were divided based on type of data used (raw abundance, relative abundance and presence/absence data) and then divided by complexity of functional group class. For example, Complexity 2 refers to the use of two functional traits in forming a functional group class. Individual functional group classes are referred to by the functional traits used to form them. So, a Complexity 3 functional group class based on the traits of mobility, bioturbation and feeding, which used presence/absence data, is referred to as “Mobility-Bioturbation-Feeding Presence/Absence.”

Chl a (1), Phaeopigments (2), Depth (3), Salinity (4)
log (1+x)

Raw Abundance Data		spearman	variables	significance
	Full Species Raw Abundance	0.585	1,2,4	0.001
Complexity 4	Mobility-Size-Feeding-Bioturbation Raw Abundance	0.722	1,2,3,4	0.001
Complexity 3	Size-Feeding-Mobility Raw Abundance	0.5071	1,2,4	0.007
Complexity 3	Size-Mobility-Bioturbation Raw Abundance	0.732	1,2,3,4	0.002
Complexity 3	Size-Bioturbation-Feeding Raw Abundance	0.61	1,2,3,4	0.002
Complexity 3	Mobility-Bioturbation-Feeding Raw Abundance	0.552	1,2,3,4	0.007
Complexity 2	Mobility-Bioturbation Raw Abundance	0.65	1,2,3,4	0.002
Complexity 2	Size-Feeding Raw Abundance	0.558	2	0.008
Complexity 2	Size-Mobility Raw Abundance	0.725	1,2,3,4	0.001
Complexity 2	Size-Bioturbation Raw Abundance	0.847	1,3,4	0.001
Complexity 1	Bioturbation Raw Abundance	0.481	4	0.048
Complexity 1	Mobility Raw Abundance	0.781	1,3,	0.001
Complexity 1	Size Raw Abundance	0.51	1,3	0.046

Relative Abundance Data		spearman	variables	significance
	Full Species Relative Abundance	0.659	2,4	0.001
Complexity 4	Mobility-Size-Feeding-Bioturbation Relative Abundance	0.65	1,2,3,4	0.002
Complexity 3	Size-Mobility-Bioturbation Relative Abundance	0.634	1,2,3,4	0.003
Complexity 2	Bioturbation-Feeding Relative Abundance	0.501	1,2,3	0.004
Complexity 2	Size-Mobility Relative Abundance	0.558	1,3	0.018
Complexity 2	Size-Bioturbation Relative Abundance	0.681	2,3,4	0.001
Complexity 1	Feeding Relative Abundance	0.502	1,4	0.034
Complexity 1	Mobility Relative Abundance	0.71	1,3	0.001
Complexity 1	Size Relative Abundance	0.499	1,3	0.045

Presence/Absence Data		spearman	variables	significance
	Full Species Presence/Absence	0.687	1,2,3	0.001
Complexity 4	Mobility-Size-Feeding-Bioturbation Presence/Absence	0.607	2	0.008
Complexity 3	Size-Feeding-Mobility Presence/Absence	0.575	2	0.004
Complexity 3	Size-Mobility-Bioturbation Presence/Absence	0.487	2	0.029
Complexity 3	Size-Bioturbation-Feeding Presence/Absence	0.565	2	0.013
Complexity 3	Mobility-Bioturbation-Feeding Presence/Absence	0.583	2	0.015
Complexity 2	Bioturbation-Feeding Presence/Absence	0.575	2	0.013
Complexity 2	Mobility-Feeding Presence/Absence	0.595	2	0.007
Complexity 2	Size-Feeding Presence/Absence	0.558	2	0.003
Complexity 2	Size-Bioturbation Presence/Absence	0.514	2	0.029

Table 3. BIO-ENV results with significant ($p \leq 0.05$) Spearman Rank correlations that exceed the 0.5 correlation threshold. Three correlations that are slightly below the threshold are included in bold.

Presence/Absence Results

For Complexity 1, only “Feeding Presence/Absence” gave a result. It had a significant ($p=0.035$) but weak correlation ($rs=0.374$), and pinpointed phaeopigments as the single key variable. The other Presence/Absence results did not isolate any variables. For Complexity 2, all results except two were statistically significant, had correlations greater than 0.5, and put forth phaeopigments as the single key variable. For Complexity 3, all results were statistically significant, with only “Size-Mobility-Bioturbation Presence/Absence” falling short of the correlation threshold ($rs=0.487$). All pinpointed only one key variable, phaeopigments. For Complexity 4, the use of all traits (“Mobility-Size-Feeding-Bioturbation Presence/Absence”), gave a significant result ($p=0.008$), with a correlation of 0.607. It pinpointed only phaeopigments as a key variable. For species data, the result was significant ($p=0.001$), with a correlation of 0.687, and selected chlorophyll a, phaeopigments and depth as key variables. So, there is a clear difference between species and functional data. For the latter, three variables were selected by the statistical test. In contrast, the only variable that was selected for functional data, regardless of complexity, was phaeopigments.

Chl a (1), Phaeopigments (2), Depth (3), Salinity (4)	log (1+x)		
	Spearman correlation	variables	significance
Full Species Raw Abundance	0.585	1,2,4	0.001
Full species Relative Abundance	0.659	2,4	0.001
Full Species Presence/Absence	0.687	1,2,3	0.001
Mobility-Size-Feeding-Bioturbation Raw Abundance	0.722	1,2,3,4	0.001
Mobility-Size-Feeding-Bioturbation Relative Abundance	0.65	1,2,3,4	0.002
Mobility-Size-Feeding-Bioturbation Presence/Absence	0.607	2	0.008
Size-Feeding-Mobility Raw Abundance	0.5071	1,2,4	0.007
Size-Feeding-Mobility Relative Abundance	0.369	2,4	0.048
Size-Feeding-Mobility Presence/Absence	0.575	2	0.004
Size-Mobility-Bioturbation Raw Abundance	0.732	1,2,3,4	0.002
Size-Mobility-Bioturbation Relative Abundance	0.634	1,2,3,4	0.003
Size-Mobility-Bioturbation Presence/Absence	0.487	2	0.029
Size-Bioturbation-Feeding Raw Abundance	0.61	1,2,3,4	0.002
Size-Bioturbation-Feeding Relative Abundance	0.44	1,2,3,4	0.016
Size-Bioturbation-Feeding Presence/Absence	0.565	2	0.013
Mobility-Bioturbation-Feeding Raw Abundance	0.552	1,2,3,4	0.007
Mobility-Bioturbation-Feeding Relative Abundance	0.452	3	0.013
Mobility-Bioturbation-Feeding Presence/Absence	0.583	2	0.015
Bioturbation-Feeding Raw Abundance	0.409	1,2,3,4	0.073
Bioturbation-Feeding Relative Abundance	0.501	1,2,3	0.004
Bioturbation-Feeding Presence/Absence	0.575	2	0.013
Mobility-Feeding Raw Abundance	0.323	1,2,4	0.08
Mobility-Feeding Relative Abundance	0.352	1,2	0.039
Mobility-Feeding Presence/Absence	0.595	2	0.007
Mobility-Bioturbation Raw Abundance	0.65	1,2,3,4	0.002
Mobility-Bioturbation Relative Abundance	0.469	1,2,3,4	0.019
Mobility-Bioturbation Presence/Absence	0.27	1,2,4	0.144
Size-Feeding Raw Abundance	0.558	2	0.008
Size-Feeding Relative Abundance	0.473	1,2,4	0.009
Size-Feeding Presence/Absence	0.558	2	0.003
Size-Mobility Raw Abundance	0.725	1,2,3,4	0.001
Size-Mobility Relative Abundance	0.558	1,3	0.018
Size-Mobility Presence/Absence	0.582	1,2,3,4	0.968
Size-Bioturbation Raw Abundance	0.847	1,3,4	0.001
Size-Bioturbation Relative Abundance	0.681	2,3,4	0.001
Size-Bioturbation Presence/Absence	0.514	2	0.029
Feeding Raw Abundance	0.445	1,2,3,4	0.059
Feeding Relative Abundance	0.502	1,4	0.034
Feeding Presence/Absence	0.374	2	0.035
Bioturbation Raw Abundance	0.481	4	0.048
Bioturbation Relative Abundance	0.45	4	0.04
Bioturbation Presence/Absence	NA	NA	NA
Mobility Raw Abundance	0.781	1,3	0.001
Mobility Relative Abundance	0.71	1,3	0.001
Mobility Presence/Absence	NA	NA	NA
Size Raw Abundance	0.51	1,3	0.046
Size Relative Abundance	0.499	1,3	0.045
Size Presence/Absence	NA	NA	NA

Table 4. All BIO-ENV results. This includes results that were not statistically significant and results with Spearman Rank correlations less than the 0.5 threshold. In three cases, no results could be obtained at all (labeled “NA”).

Relative Abundance Results

For Complexity 1, all functional group classes gave significant results, but only “Feeding Relative Abundance” and “Mobility Relative Abundance” had a correlation greater than 0.5 ($rs=0.502$ and $rs=0.71$ respectively). “Size Relative Abundance” and “Bioturbation Relative Abundance” had correlations of 0.499 and 0.45, slightly below the threshold. The variable chlorophyll a was included in three out of four classes. For Complexity 2,

all functional group classes gave significant results, with “Size-Bioturbation Relative Abundance,” “Size-Mobility Relative Abundance,” and “Bioturbation-Feeding Relative Abundance” giving correlations greater than 0.5. Phaeopigment was included as important in five out of six functional group classes. Chlorophyll a was also considered important in five out of six classes. Interestingly, the two variables were not always found together. For Complexity 3, all correlations were significant, but only “Size-Mobility-Bioturbation Relative Abundance” had a correlation exceeding 0.5 ($rs=0.634$). This functional group class pinpointed all four variables as important. For Complexity 4, “Mobility-Size-Feeding-Bioturbation Relative Abundance,” there was a significant ($p=0.002$) correlation of 0.65 and all variables were found to be important. For species data, the significant ($p=0.001$) correlation of 0.659 pinpointed only phaeopigments and salinity as important.

Raw Abundance Results

For Complexity 1, all correlations except “Feeding Raw Abundance” were significant ($p=0.059$). Both “Mobility Raw Abundance” and “Size Raw Abundance” had correlations exceeding 0.5 and both found chlorophyll a and depth to be the only key variables. For Complexity 2, all correlations were significant except “Bioturbation-Feeding Raw Abundance” ($p=0.073$) and “Mobility-Feeding Raw Abundance” ($p=0.073$). All significant correlations exceeded 0.5, with the greatest being 0.847 for “Size-Bioturbation Raw Abundance.” Chlorophyll a was considered important in all significant results except “Size-Feeding Raw Abundance,” which only had phaeopigments as important. In general, phaeopigments were quite important, being present in all but one of the significant results. For Complexity 3, all results had correlation coefficients greater than 0.5 and all were statistically significant. Variables chlorophyll a, phaeopigments and salinity were considered important in all functional group classes. Depth was considered important in all groups, except “Size-Feeding-Mobility Raw Abundance.” For Complexity 4, the correlation was significant ($p=0.001$) and high ($rs=0.722$). All four variables were considered important. For species data, a significant ($p=0.001$) correlation of 0.585 was found, with chlorophyll a, phaeopigment, and salinity found to be important.

Discussion

The hypothesis that more complex functional group classes, when compared to less complex classes, are closer to the use of direct species data in determining the important environmental variables was not supported by the results. More complex functional group classes did not necessarily yield better results. Some classes of lower complexity showed greater similarity to full species data. For example, a functional group class of Complexity 3, “Size-Feeding-Mobility Raw Abundance,” required only chlorophyll a, phaeopigments and salinity for the best relationship between site composition and the environment, which was also the result obtained for full species raw abundance data. The most complex functional group class, “Mobility-Size-Feeding-Bioturbation Raw Abundance,” required all four variables. Contrary to the prediction, results obtained with species data could be equivalent to a class that was not the most complex functional group class.

While establishing concrete relationships between environmental variables and site composition is a difficult task, the results could offer insights into the ecology of this benthic ecosystem. For both raw and relative abundance data, the Complexity 4 class includes bioturbation as a trait and depth as a variable, unlike with species data, suggesting this functional trait may be closely linked to depth while taxonomic composition is not. In fact, all Complexity 2 and Complexity 3 functional group classes that include bioturbation also select depth as important, at least with raw abundance data. This demonstrates why complexity is not always preferable. The functional traits that make up groups are not all equivalent. Adding a trait like bioturbation, even if it increases complexity, can create less similarity between functional and species data if the trait is not particularly important in determining how species composition varies between sites. The results also show there is no steady pattern as data complexity increases and there is no clear additive pattern for the functional traits, suggesting interactions between variables. Although the BIO-ENV results suggest each variable adds new information, the levels of chlorophyll a and phae-



opigments could be linked as both deal with primary productivity and are measures of food supply (24).

Interestingly, all useful presence/absence results for functional group classes, regardless of complexity, selected only phaeopigments as the important variable. While both phaeopigments and chlorophyll a are measures of food supply, they also differ (24). Phaeopigments, which tend to accumulate, can be seen as a measure of overall food supply. Chlorophyll a, which is more short-lived, can be considered a measure of fresh food supply (24). In fact, in Link et al. (18), the retention of chlorophyll a but not phaeopigments in their model suggested fresh food supply, rather than general food supply, was important in benthic processes. Conversely, my results suggest that overall food supply is more important when considering functional groups.

These presence/absence results are also helpful in understanding the general issue of complexity in functional group classes and its relation to taxonomic data. For presence/absence, all classes, regardless of complexity, signaled only phaeopigments. This suggests that complexity is not an important factor when it comes to presence/absence functional data. More research would be necessary to determine why this is the case, but it might be partially due to inherent limitations with using presence/absence data. Resolution is often lost, as rare and abundant species (or functional groups) are given the same weight. Removing rare species beforehand might help reduce this bias (21). The limits of presence/absence data are clearly demonstrated with Complexity 1 functional group classes, as only "Feeding Presence/Absence" gave a result. Perhaps the loss of these low complexity classes made the results appear artificially uniform.

Some information about the relationship between site composition and environmental variables is certainly lost when functional groups are used, but some appears to be retained. For instance, all meaningful results ($r \geq 0.5$, $p \leq 0.05$), regardless of complexity, retained a measure of food supply, whether chlorophyll a or phaeopigments, or both. This suggests food supply is vitally important in such ecosystems.

The results also help address the larger question of ecosystem redundancy, at least for some functional classes. For instance, the presence/absence functional group results pinpointed only phaeopigments as important, while depth was included in species results. This suggests that as depth changes, there is a significant change in species composition but not functional group composition. The species present fall into the same functional groups regardless of depth. In general, however, the results suggest that, while some redundancies exist, one must be cautious in using functional data to develop environmental policies. More research is necessary to determine which functional groups are truly comparable between distant ecosystems.

This study has certain limitations. Only four functional traits were used and more might have helped. No standard number of traits exists, the aim being enough traits to be functionally significant (1). Traits were chosen due to their importance in benthic ecosystems but choosing traits is difficult and always contains an element of subjectivity. As results show, using more traits does not guarantee more meaningful results. The results show complex trait-based systems are not necessarily reliable surrogates for taxonomy. In picking traits, researchers must balance the trait's importance with the ease of obtaining measurements (23). Also, this study used functional traits that were applied after species identification, automatically linking functional groups to taxonomy. Measuring traits beforehand would be preferable (23). Finally, only four environmental variables were used. Including more may have increased result reliability.

While more research is necessary in this field, this study helps clarify the relationship between the use of functional groups and taxonomy. The hypothesis that more complex functional group classes would approach taxonomic data when it comes to identifying key environmental variables was not supported by the BIO-ENV results. The results did offer some insight into benthic community composition. The importance of food supply in these communities was clear and the results suggested overall food supply, rather than fresh food supply, plays a key role in functional group composition, at least when looking at the presence or absence of a group. More generally, the results of this study argue caution should be taken when

using functional groups as surrogates for taxonomic data and that the assumption complexity can strengthen the reliability of such methods is unwarranted.

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