

ARTICLE

Studying biodiversity–ecosystem function relationships in experimental microcosms among islands

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Handling Editor: Nicholas J. Gotelli**Abstract**

Ecological studies on islands have provided fundamental insights into the mechanisms underlying biodiversity of larger organisms, but we know little about the factors affecting island microbial biodiversity and ecosystem function. We conducted a field experiment on five Baltic Sea islands where we placed aquatic microcosms with different levels of salinity mimicking environmental stress and allowed diatoms to colonize the microcosms via the air. Using structural equation models (SEM), we investigated the interconnections among environmental and dispersal-related factors, diatom biodiversity, and ecosystem productivity (represented by chlorophyll *a* concentration). We also tested whether the body size structure of the community influences productivity together with biodiversity. In SEMs, we found no relationship between species richness or evenness and productivity. However, productivity increased with increasing mean body size of species in the communities. The effects of environmental stress on both biodiversity and ecosystem productivity were highlighted as species richness and evenness declined, whereas productivity increased at the highest salinity levels. In addition to salinity, wind exposure affected both biodiversity metrics and productivity. This study provides new insights into microbial community assembly in a field experimental setting and the relationship between biodiversity and ecosystem function. Our results indicate that salinity presents a strong abiotic filter, leading to communities that may be species poor, yet comprise salinity-tolerant and relatively productive species at high salinity. Our findings also emphasize the importance of mean community body size in mediating the effects of environmental conditions on productivity and suggest that this trait should be considered more broadly in biodiversity–ecosystem function studies.

KEYWORDS

biodiversity–ecosystem function, body size, chlorophyll *a*, diatoms, evenness, islands, productivity, salinity, species richness

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INTRODUCTION

One of the most stunning features of Earth is the biodiversity and its ecological and evolutionary drivers (Brown, 2014; Tilman, 1977). To investigate the drivers of biodiversity, islands provide ideal model systems and insights derived from islands have inspired the development of foundational theories in ecology and evolution (MacArthur & Wilson, 1967; Warren et al., 2015; Whittaker et al., 2017). As discrete entities, islands serve as particularly fruitful venues to examine the roles of local and regional factors in shaping biodiversity. Whereas island studies focusing on macroorganisms have greatly increased our understanding of the mechanisms influencing biodiversity, little information is known about the patterns and determinants of island biodiversity and community assembly for microorganisms (Li et al., 2020; Wang et al., 2019), which are key players for various ecosystem functions (e.g., Hope et al., 2020).

In addition to exploring the patterns and drivers of biodiversity, the functional consequences of biodiversity, such as ecosystem productivity and stability and how nature contributes to human basic needs in terms of ecosystem services, have gained more attention in recent decades (Cardinale et al., 2012; Tilman, 1999). Studies examining the relationship between biodiversity and ecosystem function (BEF) have typically considered species richness as a sole indicator of biodiversity and do not consider the importance of other aspects of biodiversity. However, recently it has been shown that the fact of how total abundance is distributed among the species (i.e., evenness) may have had profound effects on ecosystem functions (Hillebrand et al., 2008; Lewandowska et al., 2016; Wilsey & Potvin, 2000). Furthermore, BEF studies are typically conducted at a local scale and lack consideration of how the larger spatial context may affect community assembly and the relationship between biodiversity and ecosystem function (Leibold et al., 2017). Some studies have, however, indicated that species dispersal processes may influence ecosystem functions, such as productivity, by affecting species richness and biotic interactions (Matthiessen & Hillebrand, 2006). Therefore, taking into account dispersal-related processes in addition to local factors would be essential to increasing our understanding of the relationship between BEF (Leibold et al., 2017).

Regarding the determinants of biodiversity, teasing apart the relative effects of local factors, such as environmental conditions, and regional dispersal processes has been problematic in observational field studies because environmental conditions typically covary with spatial gradients. Therefore, some studies have used field experimental settings to examine microbial colonization

and small-scale beta diversity patterns (Bell, 2010), to investigate how microbial communities respond to nutrient additions in different elevations and in different biomes (Wang et al., 2016), and to explore the importance of species sorting by the local environment and neutral processes during the initial assembly of microbial communities (Langenheder & Székely, 2011). To our knowledge, however, no study has examined microbial community assembly and BEF relationships experimentally among newly created habitats on islands. Here, we carried out an outdoor field experiment in which we placed aquatic microcosms covering five salinity levels on islands of the Baltic Sea and allowed diatoms (i.e., unicellular algae) to freely colonize the microcosms from air. The experimental setting therefore allowed us to examine the assembly of communities from a regional species pool into new local habitats with different levels of environmental stress in terms of salinity on true islands.

Our aim was to examine the linkages among local environmental and dispersal-related factors, diatom biodiversity, and ecosystem productivity (represented as chlorophyll *a* [Chl*a*]). Specifically, we hypothesized (H_1) that diatom species richness is influenced by spatial factors that affect species ability to disperse to new habitats and local factors that affect the colonizing species ability to persist in the local community (MacArthur & Wilson, 1967). In addition to species richness, we explored the patterns using evenness as a measure of taxonomic diversity. Species richness and evenness are often not correlated in aquatic communities (Soininen et al., 2012), emphasizing the need to consider both aspects of biodiversity for a more comprehensive understanding of biodiversity patterns. Species richness or evenness, in turn, is expected (H_2) to affect ecosystem productivity (Lewandowska et al., 2016; Tilman et al., 1996). We also examined (H_3) whether considering not only species richness and evenness, but also cell size structure of the community would be essential to identify the key determinants of productivity. Body size is typically a master trait in an ecology of species and communities correlating with, for example, species dispersal ability (Passy, 2012), the rate of life cycle (Gillooly et al., 2001) and metabolic rates (Okie et al., 2013). Within communities, the community body size structure may be influenced by the local environmental conditions (Finkel et al., 2009; Svensson et al., 2014); therefore, we also (H_4) expected to find connections between the local environmental variables and the average body size of the species in communities, which would then drive productivity jointly with richness or evenness. Furthermore, we expected that the local environmental conditions and dispersal-related factors may influence ecosystem productivity both directly and indirectly by affecting the species richness, evenness, and the mean body size.

We explored these relationships using a structural equation modeling (SEM) approach, which allowed one to represent and evaluate hypotheses regarding causal connections in systems (Grace, 2006). In addition, we examined the roles of stochastic and deterministic processes in driving community assembly and whether the diatom community compositions within the salinity levels were as dissimilar or less or more dissimilar to each other than expected by random chance (Chase et al., 2011).

METHODS

Study area and experimental setting

The study area is located on the coast of the Baltic Sea, in southern Finland (59°48'N to 59°54'N, 23°12'E to 23°20'E) (Appendix S1: Figure S1). The field experiment was carried out on five islands between 28 May and 18 September 2019. The islands were chosen based on their position in the archipelago to include sheltered islands close to the mainland in the inner archipelago and more exposed islands farther from the mainland in the outer archipelago.

On each island, we set up 15 plastic buckets (volume 5 L), containing 3 L of water filtered through a Sartobran 0.2- μ m filter (Sartorius Stedim Biotech GmbH, Göttingen, Germany) to remove all diatoms prior to the beginning of the experiment. To facilitate sampling, 5 cm \times 5 cm tiles were added as substrates on the bottom of each bucket before the water was added. The buckets included five salinity levels, that is, 0, 3, 6, 18 and 40, and three replicates of each level. The salinity levels were chosen to correspond to naturally occurring salinities in aquatic ecosystems in and around the study region and to represent different stress levels. For the freshwater buckets, water was collected from Gennarbyviken, a sea bay that was dammed ~65 years ago to form a supply for fresh water (Räsänen & Tolonen, 1983). Gennarbyviken presents the closest, permanent large freshwater system to the study region. Water for the buckets with salinity 6 was collected from Storfjärden, a Baltic Sea pelagic area close to the study islands. The salinity level 3 was created by mixing the collected natural seawater and freshwater. Corresponding salinity (3) in natural waters occurs in an estuary close to the study region (Virta et al., 2021). The salinity levels of 18 and 40 were created by adding sea salt (Instant Ocean Sea Salt, Spectrum Brands, Blacksburg, VA, USA) to the natural seawater collected from Storfjärden. The salinity level 18 corresponds to the Kattegat in the Danish straits. The salinity level 40 was chosen to exceed the salinity of the Baltic Sea.

On each island, the buckets were placed within a wooden grid, positioned in an unshaded, open location on the surface of bare bedrock. To avoid interfering with

natural dispersal events, we did not cover the buckets with lids. To prevent direct disturbances by, for instance, water birds, we attached a net (grid size 1 \times 1 cm) on top of the buckets. These were then left on the islands to allow diatoms to colonize the microcosms via the air.

Over the course of the experiment, the buckets' water volumes varied due to precipitation and evaporation. To compensate for the loss of water during long dry periods, filtered water with the salinity levels as described above or filtered tap water was added to the buckets. Water was added on three occasions in July–August. The same volume of water was added to each bucket. The water additions prevented drying of the buckets in most cases, but on one island (Algrundet) evaporation had been unexpectedly high and resulted in a short-term drying of some of the buckets on one occasion ~10 weeks before the sampling. To test whether this affected the overall results, we constructed SEMs also with data from which we excluded all samples on the island where the drying occurred.

Field sampling and laboratory methods

The buckets were sampled at the end of the experiment in September. Diatoms were sampled from one tile per bucket by scraping the surface of the tile with a sponge (~2 cm \times 2 cm \times 2 cm). For each bucket, a separate sponge was used. From two tiles per bucket, we measured chlorophyll *a* concentration (proxy for ecosystem productivity) with a portable field instrument BenthosTorch (bbe Moldaenke GmbH, Schwentental, Germany). The BenthosTorch enables *in situ* measurement of chlorophyll *a* concentration of diatoms inhabiting benthic biofilms. Simultaneously with biofilm sampling, we measured the buckets' salinity, pH and water temperature using a Hach HQ40d multimeter (Hach, Loveland, CO, USA) and collected water samples, which were analyzed later in the laboratory for total phosphorus (TP). For the analysis of TP, subsamples of the water samples were treated with sulfuric acid and potassium peroxide sulfate and autoclaved in +121°C. A Hach Lange DR 5000 spectrometer (Hach Lange GmbH, Düsseldorf, Germany) was used to measure the TP concentrations.

Immediately after returning to the laboratory from the field, one replicate per salinity level on each island was inspected to ensure that most diatom cells were alive at the time of the sampling. Here, ~70–100 cells per sample were counted with a microscope for this purpose, separating alive and dead cells. The proportion of alive cells in the samples ranged from 70.6% to 100%; mean was 89.3%. After the samples were checked, they were preserved with ethanol and stored in the cold (+4°C) and dark until further laboratory processing.

During the sampling, we also collected a diatom sample from the closest accessible seashore to the experimental setting on each island. Five stones were randomly selected along the shoreline and diatoms were collected by scraping the stone surfaces with a sponge (25 cm² per stone) and then combined into a composite sample. The samples were collected to compare the diatom taxa recorded among the microcosms on each island to the taxa found on the littoral zone of the island. The proportion of taxa that were found in the seashore of each island and among the microcosms of the island was ~20%–25% (Unnamed island 20.8%, Algrundet 21.1%, Granbusken 21.4%, Spikarna 23.4%, Brännskär 23.5%). That is, ~20%–25% of the taxa that were recorded in the sea sample of an island were also recorded among the microcosms of that island.

Diatom analysis

In the laboratory, organic material was removed from the diatom samples using wet combustion with hydrogen peroxide (30% H₂O₂) and mounted on slides with Naphrax (Brunel Microscopes Ltd, Chippenham, UK). Then, using a phase contrast light microscope with ×1000 magnification, ~500 frustules per sample were counted and identified to the lowest possible taxonomic level. The identification followed Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Snoeijs (1993), Snoeijs and Vilbaste (1994), Snoeijs and Potapova (1995), Snoeijs and Kasperovicienė (1996), Witkowski et al. (2000), and Lange-Bertalot et al. (2017). The counts were subsequently transformed into relative abundances and species richness was calculated as the sum of all taxa observed in each bucket. Given that the observed number of species is therefore sample based, we used a rarefaction analysis to assess the relationship between species richness and counting effort. The results showed that, although counting of 500 frustules may slightly underestimate the richness of the most diverse communities, it captures well the number of species of the less diverse communities (Appendix S1: Figure S2). We therefore believe that our counting effort is overall sufficient to indicate the true patterns of diatom communities in this study. Five samples were excluded from further analyses because they had a too low cell density.

Fetch and distances to potential source pools

As spatial factors and proxies for dispersal-related effects, we use measures of wind exposure and distances to potential source species pools. To account for differences in wind exposure among the islands, we calculated fetch,

that is, the distance that wind can travel across open water. Fetch was calculated by measuring the shortest distance to the next shore, island or islet along 40 lines at 9° intervals, the beginning point of which was placed at the shore that was closest to the experimental setting on each island in the most common wind direction of the study region (i.e., southwest). The mean of the obtained 40 values was used as a measure of fetch for each island (modified from Mason et al., 2018). Fetch therefore represents wind exposure and provides a proxy for connectivity to potential littoral source pools surrounding the study settings. The distance measurements were done using the ruler tool in Google Earth (Google, 2021).

Distance to the coastal source pool was measured as the shortest distance to the coast of mainland of Finland from the location of the experimental setting on each island. The distances were measured using digital maps and orthophotographs. We hypothesize that the distance to the coastal pool may influence species richness because of the extensive benthic littoral habitats along the coastline of the mainland and the proximity of inland freshwater habitats. If these systems serve as important source pools, species richness would be higher on islands closer to the coastal pool than on more distant islands farther from the mainland.

Within each island, we measured *in situ* the shortest distance to the closest seashore from the experimental setting. We also measured the distances to 10 closest rock pools and calculated their mean to represent the distance to rock pools on each island. Rock pools among these islands provide small aquatic habitats, which harbor diatom communities along a freshwater to brackish transition (Teittinen & Virta, 2021) and may therefore serve as diatom source pools for the microcosms.

Statistical analyses

In the statistical analyses, we used two measures of biodiversity, that is, species richness and Pielou's evenness (Pielou, 1966). Mean body size of the species in communities (from this point forwards, mean community biovolume) was calculated as the sum of biovolumes of the cells counted divided by the total number of cells counted for each sample. The biovolumes for each species were obtained from the literature (Rimet & Bouchez, 2012; Snoeijs et al., 2002). From the calculation of mean biovolume, eight taxa rare in these data were excluded because no biovolume data were available for them. The chlorophyll *a* concentration of diatoms (mean of the two tiles) was used as a proxy for productivity. For the chlorophyll *a* concentrations that were below the limit of 0.01 µg/cm², we used value 0.005 µg/cm².

Prior to the SEMs, TP, mean biovolume, and chlorophyll *a* were log₁₀-transformed owing to their skewed distributions. Spearman’s rank correlation coefficients (r_s) were used to assess statistical dependence between the variables. Distance to the sea was strongly correlated with distance to the coastal source pool ($r_s = 0.79$) and fetch with distance to rock pools ($r_s = 0.90$). The effects of these variables were therefore tested separately in the subsequent SEMs. All other pairwise correlations were $r_s \leq 0.7$; therefore, all other variables were considered in the initial models.

Then, we first explored the relationships between each response and explanatory variable with simple linear regressions and constructed models that comprised quadratic terms of the explanatory variables to detect nonlinear relationships. The relationships between salinity and species richness and salinity and evenness were clearly unimodal. To take into account these nonlinear patterns, composite variables were created for the paths: species richness ~ salinity and evenness ~ salinity. The composite variables were created by extracting the coefficient estimates of linear and polynomial terms of salinity and subsequently multiplying the linear and polynomial terms by their estimates and then including them as combined in the SEMs.

SEMs were then constructed to examine the relationships among local environmental and spatial variables, species richness/evenness, mean community biovolume, and chlorophyll *a*. SEMs were built separately using either species richness or evenness as the biodiversity metric. First, we constructed initial models, which comprised all hypothesized pathways between the response and explanatory variables. To assess variable importance among the correlated spatial variables, we built separate SEMs using different combinations of these variables. We considered initial models with a fit $p > 0.05$ as candidate models and chose the model with the lowest Akaike information criterion (AIC) as the best-fit initial model (please refer to Appendix S1: Table S1 for AIC of the considered models). In the selected best-fit initial models, fetch and distance to the sea were included as spatial variables, and the original salinity values and TP as local environmental variables (Figure 1). We included TP as a local environmental variable in addition to salinity because the microcosms were open systems to allow colonization and naturally exposed to external nutrient inputs carried by, for instance, birds in the archipelago. Such effects may have been stronger on some islands than others. In the data exploration prior to fitting the SEMs, we indeed noticed differences in the TP concentrations among the islands (Appendix S1: Figure S3). From the initial models, nonsignificant paths were removed stepwise until all paths were significant. Goodness-of-fit

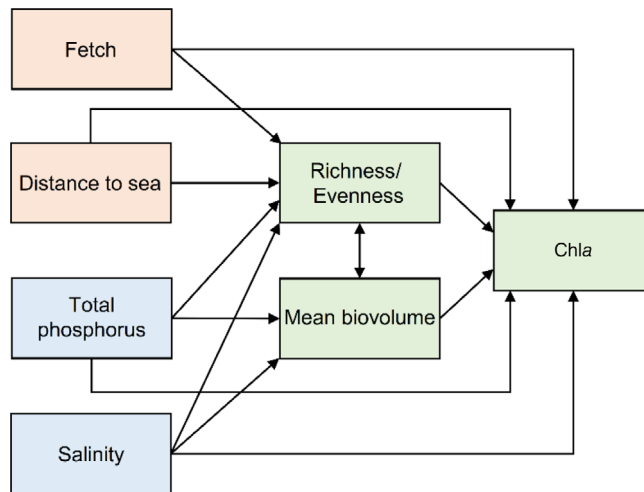


FIGURE 1 A conceptual model showing the hypothesized relationships among the spatial and environmental variables, biodiversity, mean community body size (biovolume) and chlorophyll *a* (Chla; proxy for ecosystem productivity) for benthic diatom communities in the experimental microcosms

of the models were assessed using Fisher’s C statistic and models with $p > 0.05$ indicate a good fit. The SEMs were built using R package *piecewiseSEM* (Lefcheck, 2016). The SEM results using the data with four islands (Appendix S1: Figure S4) were highly similar as with the data comprising all five islands. Therefore, we show here the results using the full data with five islands.

Additionally, to assess whether the SEM results depended on the diversity metric, we ran the initial best-fit models using effective number of species (calculated as the exponential of the Shannon–Wiener index; Jost, 2006) as the measure of diversity. As the SEM results using the effective number of species (log₁₀ transformed) (Appendix S1: Figure S5) were similar to the results obtained using the observed species richness and evenness, we showed here the results using the observed richness and evenness. To investigate the relationship between the observed species richness and evenness, we used linear regression.

Finally, to test whether the diatom communities were stochastically (e.g., related to stochastic dispersal or ecological drift) or deterministically (i.e., related to abiotic or biotic filtering) assembled, we used the null model approach proposed by Chase et al. (2011). By using the R code provided by Chase et al. (2011) with 9999 randomizations, we calculated pairwise Raup–Crick dissimilarities (β_{RC}) based on presence–absence data that included all communities among the microcosms. From the produced distance matrix, we extracted all pairwise dissimilarities within each salinity level. Then, we calculated the mean β_{RC} of all pairwise dissimilarities within each

salinity level and used a t -test to assess whether it was significantly different from zero. The β_{RC} values can vary from -1 to 1 . Mean β_{RC} values close to zero indicate stochastic community assembly. Mean β_{RC} values approaching -1 indicate that communities are deterministically assembled and less dissimilar than expected by random chance. Alternatively, mean β_{RC} values approaching 1 denote that communities are deterministically assembled and more dissimilar to each other than expected by chance. All statistical analyses were conducted in R version 4.0.5 (R Core Team, 2021).

RESULTS

Species richness in the microcosms varied between 2 and 17 (mean: 8) and evenness between 0.02 and 0.83. Mean community biovolume ranged from 18.0 to 579.9 μm^3 . Distance to the coastal source pool ranged from 0.04 to 2.9 km and fetch from 0.23 to 48.06 km. Distance to the sea ranged from 4.3 to 4.8 m on the sheltered islands and from 13.7 to 37.5 m on the exposed islands. Mean distance to rock pools varied between 7.2 and 18.5 m. Total phosphorus varied between 46 and 2716 $\mu\text{g L}^{-1}$ (mean: 415.9).

There was a significant unimodal relationship between salinity and species richness ($R^2 = 0.15$, $p = 0.005$; Figure 2a) and between salinity and evenness ($R^2 = 0.14$, $p = 0.007$; Figure 2b), whereas the relationship between salinity and diatom chlorophyll a was positive ($R^2 = 0.22$, $p < 0.001$; Figure 2c).

The SEM which included species richness indicated that richness was directly affected by salinity (unimodal), fetch (negative effect), and TP (negative effect) (Figure 3a). No significant relationship between species richness and chlorophyll a was found. Chlorophyll a was influenced directly by mean community biovolume, salinity, and

fetch, all of which had positive effects. Mean biovolume was directly affected by TP (negative effect) and salinity (positive effect). Mean biovolume and species richness were positively correlated with each other. The model (Fisher's $C = 12.39$, $p = 0.415$) explained 47% of variation in chlorophyll a , 43% of variation in species richness, and 56% of variation in mean community biovolume. Distance to the sea had no significant effects and it was excluded from the final model.

When evenness was used as the biodiversity metric, the SEM results were highly similar to the SEM that included species richness, except that evenness was directly affected only by salinity (unimodal) and fetch (negative effect) (Figure 3b). There was no significant relationship between evenness and chlorophyll a . The model (Fisher's $C = 11.32$, $p = 0.661$) explained 47% of variation in chlorophyll a , 33% of variation in evenness, and 56% of variation in mean community biovolume.

Based on linear regression, there was a significant positive relationship between species richness and evenness ($R^2 = 0.22$, $p < 0.001$).

The mean β_{RC} values within the salinity levels were negative, ranging from -0.309 within the salinity level 0 to -0.853 within the salinity level 40 (Figure 4). For each salinity level, the mean β_{RC} was significantly different from zero (t -test, all $p < 0.001$).

DISCUSSION

To our knowledge, this is the first study to explore the connections among environmental and spatial variables, biodiversity, body size structure of the community and productivity using microbial communities assembled from the regional species pool into newly created experimental ecosystems on true islands. As hypothesized (H_1),

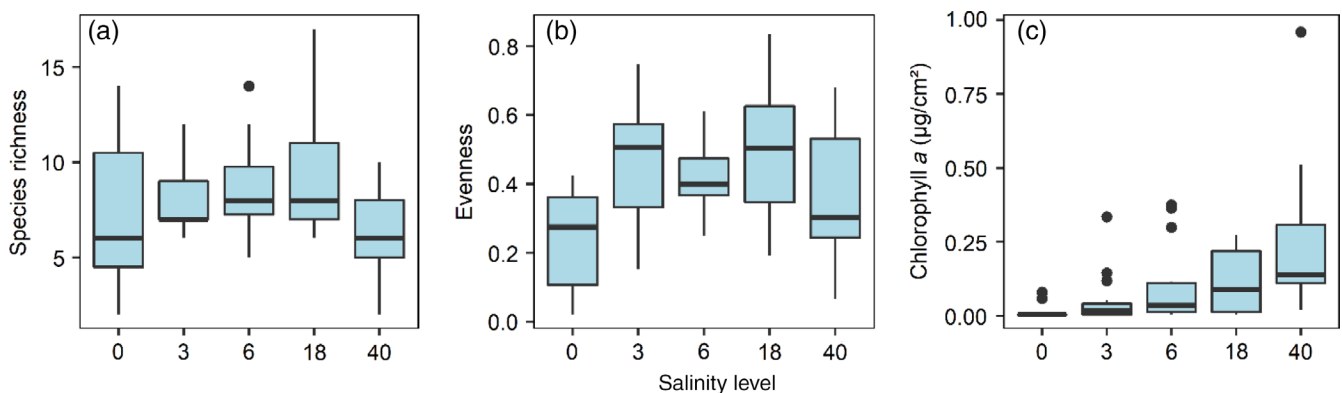


FIGURE 2 Boxplots illustrating (a) species richness, (b) evenness, and (c) chlorophyll a at different salinity levels for benthic diatoms in the experimental microcosms. Salinity levels were chosen to correspond to naturally occurring salinities in aquatic ecosystems in and around the study region and to represent different stress levels

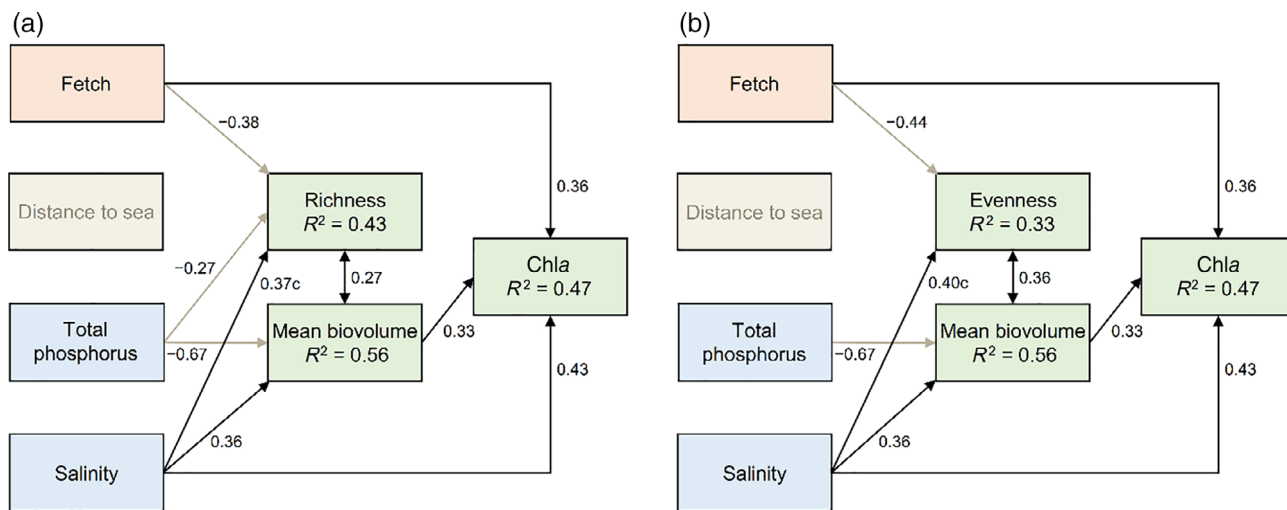


FIGURE 3 Structural equation models exploring the relationships between spatial and environmental variables, (a) species richness and (b) evenness, mean community biovolume, and chlorophyll *a* (Chla) for benthic diatom communities in the experimental microcosms. Black arrows indicate significant positive or unimodal (c) effects and gray arrows indicate significant negative effects. Double-headed arrows indicate significant correlative relationships. The values corresponding to the paths are standardized path coefficients. R^2 values showing the amount of explained variation are given for the response variables. Distance to the sea was excluded from the final models because it had no significant effect in the models

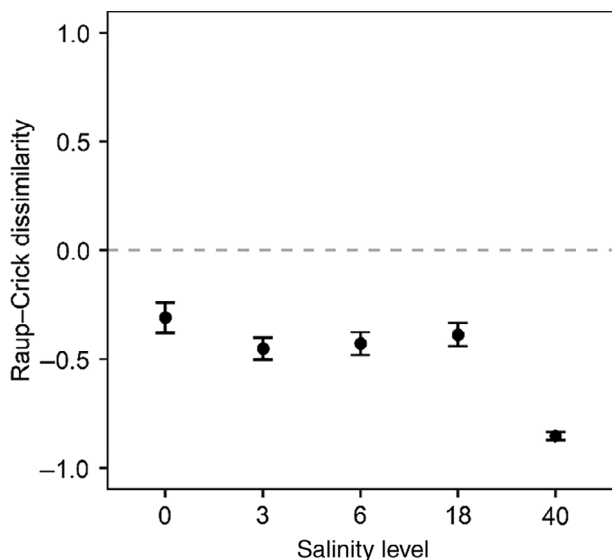


FIGURE 4 Raup-Crick dissimilarities (mean \pm SE) for benthic diatom communities within different salinity levels in the experimental microcosms

species richness was influenced by the local environmental and spatial factors. In the SEMs, species richness was most strongly influenced by salinity and fetch. Along the salinity gradient, the number of species tended to be higher in the brackish systems compared with the low and high salinity systems. This outcome contrasted with recent findings for benthic diatoms (Virta et al., 2020) and phytoplankton (Olli et al., 2019) in the Baltic Sea,

showing a richness minimum at intermediate salinities of ~5–6 and 7–9, respectively. Along a continuum from freshwater to marine conditions, the diversity minimum at intermediate salinities may reflect the fact that, on a global scale, brackish habitats are isolated from each other and have limited connectivity as they are confined to regions between the freshwater and marine realms (Olli et al., 2019). Interestingly, the unimodal richness-salinity relationship found here is also completely opposite to the Remane curve (Remane, 1934), suggesting that species richness minimum generally occurs at salinities of ~5–8, reflecting the inability of both freshwater and marine species to adapt to brackish waters. Although the findings of the present study are, of course, not directly comparable with those originating from observations on relatively stable, natural ecosystems and salinity continua, they may share similar underlying mechanisms. Here, the highest salinity level greatly exceeded that of any nearby natural waters and the lower number of species in these systems may stem from the combined effects of high level of environmental stress for most species in the regional species pool and long distances to potential source pools with similar salinity.

In addition to the high salinity systems, the freshwater microcosms had generally lower richness Chla compared with the brackish ones, although the number of species in the fresh waters showed higher variability compared with the high salinity systems. This finding could indicate that colonization of species tolerating low salinity is hindered by the distances to potential immigration sources

(MacArthur & Wilson, 1967). However, although the distance to the coastal source pool showed a negative association with species richness when tested with linear regression prior to SEM, it was not included in the best-fit final SEM. The apparent distance effect therefore seems to reflect the effects of other variables more directly influencing richness, such as TP, the concentrations of which were particularly high in some occasions on islands located farther from the mainland. The nutrient enrichment probably stems from the effects of occurrence of seabird populations typical for some of the islands in the archipelago. As we did not cover the experimental ecosystems with lids to allow natural dispersal events, they were naturally also exposed to possible allochthonous nutrient inputs. It has been shown that nutrient fluxes carried by waterbirds across habitat boundaries can substantially increase nutrient concentrations and affect the dynamics of the receiving ecosystems (Anderson & Polis, 1999). The effects of seabirds as vectors profoundly influencing chemistry and biota of recipient island aquatic ecosystems have also been highlighted (Duda et al., 2021).

Species richness also decreased with increasing fetch, that is, wind exposure. In the Baltic Sea coastal region, wind exposure shapes benthic diatom community composition (Virta et al., 2021) and a lower number of species in diatom communities has also been linked to higher wave exposure (Busse & Snoeijs, 2003). As the experimental systems were, however, protected from the direct effects of wind-induced wave disturbances, the effect of fetch reflected some other underlying mechanisms. Although the reason for the effect of fetch on species richness is speculative, it may be that as the sheltered islands share a higher proportion of shoreline and, therefore, littoral benthic habitats, of the other islands and/or the mainland, the higher proportion of potential source pools could potentially further increase the chance of colonization and subsequently the number of species. The effect of fetch may also partly reflect decreasing richness with increasing distance to the surrounding rock pools, because fetch correlated positively with distance to rock pools, which may serve as source pools for the microcosms.

Noteworthy, the diatom species richness in the microcosms was lower than the richness of the sea samples collected from the littoral of each island and the richness of diatom communities observed in natural rock pools on these islands (Teittinen & Virta, 2021). The lower richness may be explained using several ways of reasoning. First, the isolated nature of the microcosms may limit species dispersal, especially among rare species that typically have low relative abundances and therefore presumably a lower probability of successful airborne colonization as species

local abundance and regional occupancy are often positively correlated (Soininen & Heino, 2005). Second, although the experiment lasted for the entire summer period from May to September, the exposure time may have been too short for all potential species in the regional species pool to reach these newly formed habitats. Third, salinities were not stable over the duration of the experiment and occasionally during extended dry periods, they increased from the original salinity levels, requiring therefore high salinity tolerance from the species able to maintain viable populations. Fluctuating salinities may have therefore excluded species that were sensitive to salinity variation, leading to communities comprised of species that have broad tolerances toward salinity. Furthermore, given the relatively small volume of the microcosms, temporal temperature fluctuations may have also been large, possibly limiting the number of species that are able to survive under such variable conditions.

Interestingly, evenness showed highly similar patterns as did species richness in response to salinity and fetch and there was also a positive relationship between these biodiversity metrics. Similarly, mostly positive relationships between richness and evenness have been recently reported for stream biofilm microbes (i.e., bacteria and diatoms), implying that the two aspects of biodiversity may be driven by similar underlying mechanisms (Wang et al., 2017). In contrast, no consistent richness–evenness relationships were observed in a study on terrestrial plants, suggesting that they were shaped by different ecological processes and that the relationship between richness and evenness can be site specific (Ma, 2005). A meta-analysis of richness–evenness relationships across aquatic ecosystems also showed that richness and evenness are often not correlated and concluded that this relationship is highly context dependent, contingent on both organismal and environmental characteristics (Soininen et al., 2012). In this study, however, richness and evenness seem to share similar driving mechanisms such that, coupled with potential dispersal limitations, stressful environmental conditions led to species-poor communities dominated by one or a few tolerant species. In particular, environmental filtering may decrease the number of species by excluding species sensitive to stress and decrease evenness because tolerant species only are able to maintain large populations (Passy et al., 2017).

Regarding the relationship between species richness or evenness and productivity, our results contradicted our hypothesis (H_2) as, according to SEM, there was no relationship between diatom species richness or evenness and chlorophyll *a*. Our results therefore disagreed with many studies that have found significant relationships between species richness and productivity (e.g., Hector et al., 1999; Tilman et al., 1996). Some studies have also

highlighted the importance of species evenness for productivity. For example, Wilsey and Potvin (2000) reported that decreases in terrestrial plant evenness may cause indirect decreases in plant productivity. It should be noted, however, that in nonexperimental, naturally assembled communities, the relationships between biodiversity and ecosystem functioning can be highly variable (Hagan et al., 2021; van der Plas, 2019) and that comparing the results of experiments that manipulated diversity with nonmanipulative experiments is not straightforward. Interestingly, in the present study, species richness and evenness showed a unimodal relationship with salinity, whereas the relationship between chlorophyll *a* and salinity was positive. These results suggested that, whereas the conditions at the highest salinity level constrained the number of species, they also selected for some salinity-tolerant species that were capable of relatively high productivity. In addition to salinity, productivity was directly and positively influenced by fetch, the effect of which may be linked to differences in dispersal rates among islands and possibly to a higher number of dispersing individuals on the more exposed islands in the outer archipelago.

The results further showed that productivity was indirectly influenced not only by salinity, but also by TP concentrations, through their effects on the community body size (i.e., biovolume) structure. As hypothesized (H_3), the mean community body size influenced productivity directly, with communities that comprised larger species generally supporting higher productivity compared with communities that comprised small species. Body size therefore appeared to be a key trait in these systems, mediating the effects of environmental conditions on ecosystem productivity and being a more important community characteristic for productivity than richness or evenness. These findings broadly agreed with earlier reports that have emphasized organism body size as an important trait, the consideration of which provides essential knowledge about the mechanisms that underlie ecosystem functioning (Norkko et al., 2013; Reiss et al., 2011).

Along the environmental gradients, the mean community body size decreased with increasing TP concentration and increased with increasing salinity. This outcome therefore agreed with the expected relationship between body size and local environmental conditions (H_4). The negative association between mean diatom size and TP observed here disagreed with observations of Lavoie et al. (2006), who found no relationship between average benthic diatom size and TP in streams and creeks in Canada. Finkel et al. (2009) reported that the relationship between diatom community size structure and TP differed among lake planktonic, periphytic, and benthic communities, such that the size of planktonic species decreased with increasing nutrient concentrations, whereas

no significant relationships were detected for benthic or periphytic diatom communities. Changes in mean community cell size have also been suggested to emerge from the combined effects of nutrients and salinity. In a study conducted along a Baltic Sea salinity gradient, average benthic diatom community cell volume decreased with decreasing salinity, the effect of which was presumably influenced by nutrient stoichiometry (Svensson et al., 2014). Furthermore, marine and freshwater environments have been shown to exhibit different diatom size distributions, with freshwater diatoms being significantly smaller than their marine counterparts (Litchman et al., 2009).

In addition to affecting diatom diversity, cell size, and productivity, salinity influenced the relative importance of stochastic and deterministic processes in community assembly. Overall, the mean Raup–Crick dissimilarities within all salinity levels were significantly lower than expected based on random chance alone. The results therefore suggested that environmental filtering led to more similar community compositions within the salinity levels than expected if stochastic processes dominated the structuring of communities. Notably, the relative importance of deterministic processes was by far the strongest in the highest salinity level, implying that environmental filtering was strongest under such extreme conditions. Our findings agreed with previous studies that have indicated a stronger influence of deterministic processes on microbial communities in more extreme environments (Stegen et al., 2012; Wang et al., 2012).

Whereas our study was focused on exploring the effects of salinity on diatom communities, the salinity gradient may naturally affect other organisms too. A limitation of our study is that we did not consider the potential effects of biotic interactions, especially grazing, on the observed patterns. For example, rock pools on the islands in this archipelago harbor populations of *Daphnia* species, which passively disperse among the rock pools (Pajunen & Pajunen, 2003). They could potentially also colonize the microcosms and exert a top-down control on the diatom communities. For instance, decreasing grazing pressure with increasing salinity level could possibly contribute to the increasing productivity with salinity. Such effects are, however, highly speculative at present, and we encourage future studies to specifically investigate the effects of trophic interactions on microbial communities in field experimental settings.

In conclusion, this study provides new insights on microbial community assembly into newly formed isolated habitats and subsequent community responses to environmental stress using field experiments on true islands. We found no support for species richness or evenness in driving ecosystem productivity. Instead, the community body size structure was a stronger

determinant of productivity, with communities that comprised larger species being generally more productive than communities that comprised small species. The results emphasized the effects of environmental stress in terms of salinity in shaping both species diversity and productivity. At the highest salinity levels, both richness and evenness tended to decrease, whereas productivity increased, perhaps suggesting that high salinity presented a strong abiotic filter, selecting for some salinity-tolerant species capable of relatively high productivity. In addition, wind exposure and distances to potential littoral source pools emerged as important drivers of species diversity and productivity. Furthermore, salinity and nutrient concentrations strongly affected the community body size structure, as mean size increased with salinity and decreased with TP. The results indicated that body size is an important trait for characterizing communities and mediating the effects of environmental factors on productivity. Therefore, considering the mean community body size in addition to diversity may be essential in order to unravel the mechanisms driving productivity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Teittinen et al., 2022) are available in Dryad at <https://doi.org/10.5061/dryad.crjdfn35q>.

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