

1 **Vertical and lateral distribution of Foraminifera and Ostracoda in the East Frisian**
2 **Wadden Sea – developing a transfer function for relative sea-level change**

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13 Running title: Foraminifera and Ostracoda in the East Frisian Wadden Sea

14 **Abstract**

15 In light of rising sea levels and increased storm surge hazards, detailed information on relative
16 sea-level (RSL) histories and local controlling mechanisms is required to support future
17 projections and to better prepare for future coastal-protection challenges. This study
18 contributes to deciphering Holocene RSL changes at the German North Sea coast in high
19 resolution by developing a transfer function for RSL change. Recent associations of
20 Foraminifera and Ostracoda from low intertidal to supratidal settings of the barrier island of
21 Spiekeroog in combination with environmental parameters (granulometry, C/N, TOC,
22 salinity) were investigated and quantified in elevation steps of 15 cm in order to generate a
23 first transfer function (TF) of Holocene RSL change. In a future step, the TF can be applied to
24 the stratigraphic record. Our data show a clear vertical zonation of foraminifer and ostracod
25 taxa between the middle salt marsh and the tidal flat with very few individuals in the sand flat
26 area, suggesting removal by the tidal current or poor preservation. Multivariate statistics

27 identify the elevation, i.e. the inundation frequency, as main driving factor. The smallest
28 vertical error (49 cm) is associated with an entirely new approach of combining Foraminifera
29 and Ostracoda for a TF. Advantages of the TF over classical RSL indicators such as basal and
30 intercalated peat – beside the relatively narrow indicative meaning – include the possible
31 application to a wide range of intertidal facies and that it does not depend on compaction-
32 prone peat.

33 **Keywords:** North Sea, Holocene, microfauna, ecology, relative sea-level history, Spiekeroog,
34 back-barrier tidal flats, Germany

35 **1 Introduction**

36 Relative sea-level (RSL) reconstructions are essential for understanding past and recent
37 coastal processes and represent a crucial framework for future predictions of sea-level rise
38 (Woodroffe & Murray-Wallace, 2012). This information is urgently needed for all fields of
39 coastal zone management and the mitigation of coastal hazards – in particular in light of rising
40 sea levels and a future increase of storm surge levels (Weisse et al., 2012; Rahmstorf, 2017) –,
41 as well as in the fields of basic coastal research (e.g. geomorphology, sedimentology,
42 palaeoclimatology, geoarchaeology) (Overpeck et al., 2006; Nicholls & Cazenave, 2010). The
43 reconstruction of Holocene RSL changes along the German North Sea coast, until now, is
44 mostly based on basal and intercalated peats (e.g. Behre & Streif, 1980; Behre, 2007) and
45 shows rather coarse vertical resolution. Several authors have expressed the need for more
46 precise quantitative data (Vink et al., 2007; Bungenstock & Schäfer, 2009; Bungenstock &
47 Weerts, 2010, 2012; Baeteman et al., 2011; Meijles et al., 2018).

48 A high-resolution reconstruction of past local RSL changes can be achieved by means
49 of analysis of fossil salt-marsh Foraminifera, shell-bearing protists, which create very specific
50 assemblages in the sedimentary record based on habitat conditions. A dense dataset of taxa
51 distribution along a vertical transect of local modern intertidal environments can be used to
52 develop a transfer function (TF), which models the relation between elevations of sample

53 points and relative abundances of foraminifer species over time. Such a TF may permit
54 inferences of palaeo-water depths with a centimetre-scale precision (Leorri et al., 2010; Kemp
55 et al., 2012; Edwards & Wright, 2015), but typically within ~10–15% of the tidal range,
56 leading to a decimetre-scale precision for mesotidal environments (cf. Barlow et al., 2013).
57 The use of salt-marsh Foraminifera for local relative sea-level reconstructions has been
58 established during the last two decades especially in North America, Denmark and on the
59 British Isles (e.g. Scott et al., 2001; Gehrels & Newman, 2004; Gehrels et al., 2002; Pedersen
60 et al., 2009; Engelhart & Horton, 2012; Kemp et al., 2013), but so far, applications are lacking
61 for the southern part of the German Bight. Besides Foraminifera, Ostracoda, small crustaceans
62 with a bivalved calcified carapace, occur within the same sediment fractions in the wider
63 study area (Scheder et al., 2018). We assume that Ostracoda may provide additional
64 information for more detailed reconstructions for the lower intertidal and uppermost subtidal.
65 For the first time in palaeo-sea-level research, we combine Foraminifera and Ostracoda for a
66 RSL TF (relative-sea-level transfer function).

67 This study presents the vertical zonation of recent living and dead Foraminifera and
68 Ostracoda along a cross-shore profile in the back-barrier tidal flat of the East Frisian barrier
69 island of Spiekeroog as an initial step of a transfer-function-based RSL reconstruction.
70 Foraminifera and Ostracoda distribution is interpreted in light of tidal influence and
71 sedimentary environments and translated into a first RSL TF. Research hypotheses are:

- 72 I. A vertical and lateral zonation of associations of foraminifers and ostracods
73 mainly depends on elevation, hence, the duration of water cover.
- 74 II. The additional use of ostracods for TF development leads to an improvement
75 compared to the common procedure of using exclusively foraminifers.
- 76 III. A foraminifer and ostracod based TF provides a more precise vertical
77 resolution of sea-level index points than so far used at the German North Sea
78 coast.

79 **2 Study area**

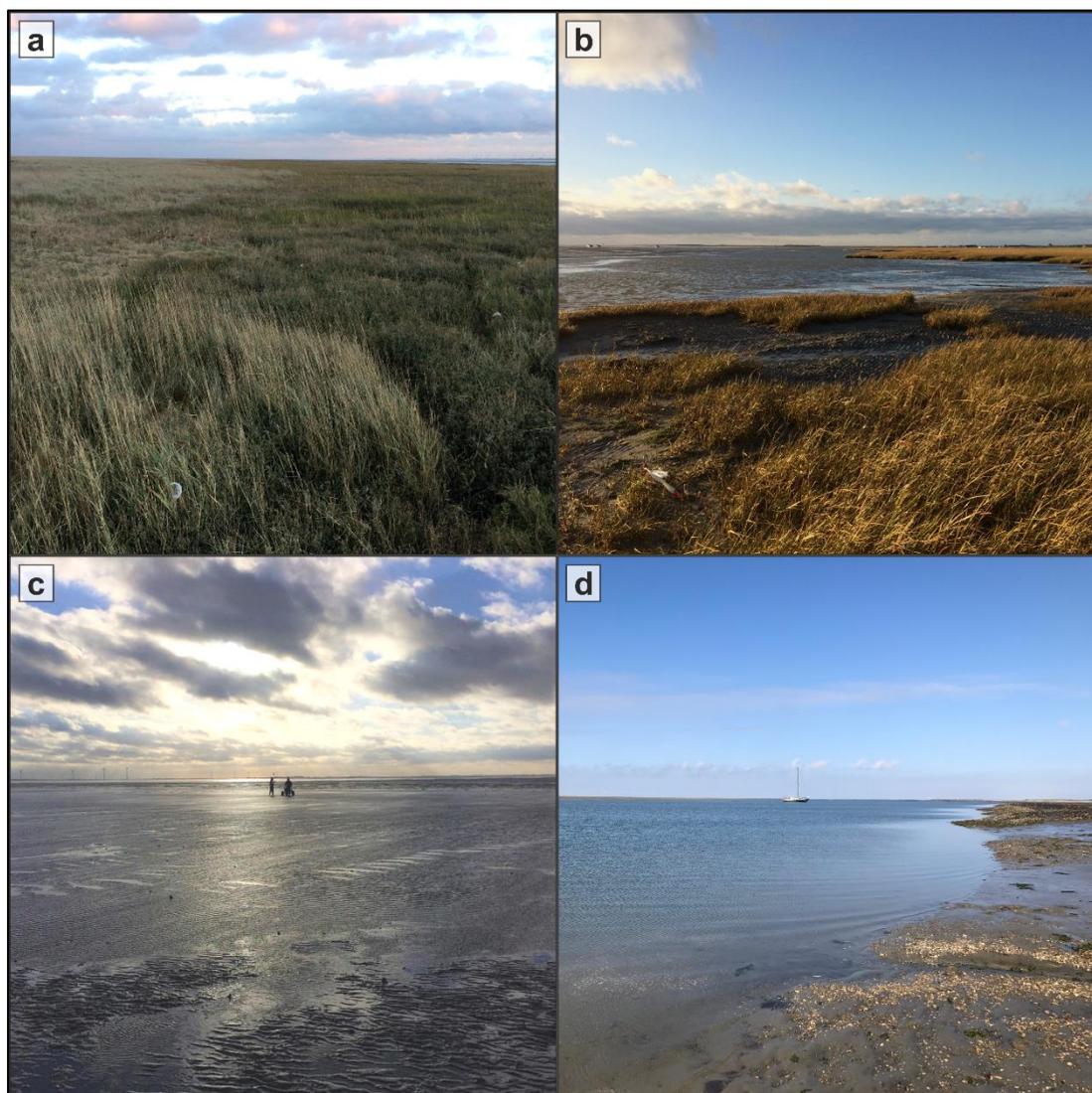
80 The study area is situated at the southern coast of Spiekeroog (see Fig. 1), one of the East
81 Frisian barrier islands, which developed after around 6–7 ka BP (kiloyears before present, i.e.
82 before AD 1950) when post-glacial sea-level rise decelerated (Behre, 1987; Freund & Streif,
83 1999; Flemming, 2002; Bungenstock & Schäfer, 2009). Due to ongoing relative sea-level rise
84 and prevalent longshore current directions, the barrier islands have shifted over several
85 kilometres in a south-easterly direction since their formation (Streif, 1990; Flemming, 2002),
86 reaching their recent position about 2000 years ago (Freund & Streif, 2000). Diurnal tides
87 (mean tidal range = 2.7 m, BSH 2018) fill and empty the back-barrier mesotidal prism of
88 Spiekeroog through the two tidal inlets Otzumer Balje and Harle. The tidal flat merges
89 towards the island and transforms into a well-developed salt marsh. The area is characterised
90 by a humid tempered climate (Cfb after latest Köppen-Geiger classification; Kottek et al.,
91 2006; Beck et al., 2018) with mean winter temperatures between 2.9 and 5.7 °C and mean
92 summer temperatures between 15.8 and 18.3 °C (weather station Wangerland-Hooksiel,
93 survey duration: 2014–2019). The salinity lies around 30 psu (practical salinity units) close to
94 the main tidal channel (southeast of the island) and a little lower towards the mainland. After
95 occasional freshwater input (e.g. heavy rainfall events), the salinity can decrease to less than
96 25 psu (Kaiser & Niemeyer, 1999; Reuter et al., 2009).



97

98 **Figure 1.** Overview of the study area. a: The southern North Sea coast with the East Frisian Islands
 99 (Spiekeroog is framed). b: The backbarrier area of Spiekeroog with the investigated surface transect at
 100 the southern coast of the island reaching from the salt marsh to the nearest tidal channel ‘Swinn’ (map
 101 source: Esri, Digital Globe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS,
 102 AeroGrid, IGN, and the GIS User Community).

103 Due to the shore-normal energy gradient (cf. Nyandwi & Flemming, 1995) an
 104 offshore-coarsening trend in grain sizes is observed. This general trend can be locally
 105 interrupted by tidal channels, depressions or old channel fillings (Bungenstock et al., 2002),
 106 whereas the barrier islands do not disturb it, thus, there is no shoreward fining trend in grain
 107 size in the southern salt marshes of the island. Therefore, sampling in the opposite direction
 108 from the island’s salt marshes down to the low water line in the back-barrier tidal flat
 109 generally results in sampling from sand flats to finer-grained mixed flats. The investigated
 110 transect (c. 1180 m in N-S direction, directly bordering the national park area) covers the
 111 natural salt marsh and adjacent back-barrier tidal flat of the island reaching the nearest tidal
 112 channel ‘Swinn’ in the south (see Figs. 1 and 2). The vegetation above and along the transect
 113 shows a more or less characteristic pattern from the high to middle salt marsh (sea lavender
 114 [*Limonium vulgare*]) crossing the ‘Andel’ Zone (lower salt marsh; andel grass [*Puccinellia*
 115 *maritima*], salt bush [*Atriplex halimus*]) and the Glasswort Zone (Pioneer Zone; cord grass
 116 [*Spartina anglica*], glasswort [*Salicornia europaea*]) down to the Seagrass Zone (tidal flat;
 117 seagrass [*Zostera*]) (cf. Streif, 1990; Gerlach, 1999).



118

119 **Figure 2.** Photographic documentation of the study area during low tide. a: transition between middle
 120 and lower salt marsh (view towards SE); b: transition between salt marsh (pioneer zone) and sand flat
 121 (view towards W); c: view from the sand flat to the mixed flat (view towards S); d: margin of the tidal
 122 channel ‘Swin’ (view towards SW).

123 **3 Methods**

124 **3.1 Field work**

125 Twenty-three samples were taken during low tide (nineteen in December 2015 [neap-tide
 126 situation, 9–10 °C, dry weather], additional four in July 2017 [spring-tide situation, 15–20 °C,
 127 c. 1 mm of rainfall before sampling]) along a transect reaching from shallow subtidal (tidal
 128 channel levee) to supratidal (salt marsh) areas (see Fig. 2) at the southern coast of Spiekeroog.
 129 Samples were taken in steps of 15 cm elevation difference with steel sampling rings
 130 (Eijkelkamp; diameter: 5 cm) comprising the uppermost 5 cm of the sediment surface. In

131 order to distinguish living from dead individuals, samples were conserved with rose Bengal-
132 coloured Ethanol (cf. Walton, 1952; Edwards & Wright, 2015). At each sampling point,
133 additional surface samples were taken for sedimentological analyses and, water coverage
134 provided, water samples were taken in centrifuge tubes for salinity measurements in the
135 laboratory. Elevation measurements at each sampling point were conducted using a
136 differential global navigation satellite system (DGNSS; Topcon Hiper Pro). By anchoring the
137 measured grid to the trigonometric point 2212 052 00 of the ‘Landesamt für Geoinformation
138 und Landesvermessung Niedersachsen’ (LGLN) in the Spiekeroog salt marsh, the setup
139 provides a vertical and lateral accuracy of ± 2 cm. Since the 2017 transect is slightly shifted in
140 N-S direction, samples had to be projected onto the 2015 surface profile (Fig. 3).

141 ***3.2 Laboratory analyses***

142 All microfaunal samples were carefully shaken overnight with a dispersant (sodium
143 pyrophosphate; $\text{Na}_4\text{P}_2\text{O}_7$) to prevent adhesion of clay particles and afterwards washed through
144 sieves, separating them into $>63 \mu\text{m}$ and $>100 \mu\text{m}$ fractions. For three representative samples
145 the latter was split into eight aliquots per sample using a wet splitter after Scott & Hermelin
146 (1993). From these aliquots a maximum of 200-300 individuals were counted wet in order to
147 avoid drying of organic components and damaging of agglutinated Foraminifera (cf. de Rijk,
148 1995; Edwards & Wright, 2015; Milker et al., 2016; Müller-Navarra et al., 2016). No species
149 sensitive to drying were found in these samples and no damaging of tests could be observed
150 after drying extracted individuals. Therefore, the remaining samples were air-dried, split with
151 a micro splitter (ripple divider) and counted dry. The proportion of dry-counted material was
152 weighted in order to enable extrapolation of microfaunal concentration per sample.
153 Foraminiferal species were identified based on taxonomic descriptions and illustrations in
154 Gehrels & Newman (2004), Horton & Edwards (2006) and Murray (2006), whereas
155 identification of ostracod species followed the descriptions in Athersuch et al. (1989) and
156 Frenzel et al. (2010). Because of the problem of discriminating juvenile individuals of

157 *Leptocythere*, those species were grouped under *Leptocythere* spp. for counting.
158 Discrimination of living and dead individuals was based on staining for foraminifers (at least
159 one chamber stained = living; not stained = dead) and on well preserved soft parts in
160 ostracods. The replacement of the genus *Jadammina* by *Entzia* is based on Filipescu &
161 Kaminski (2011), who regard *Entzia* as a senior synonym of *Jadammina*. Foraminifer and
162 ostracod associations were combined into a basic population for statistical analysis (100% =
163 foraminifers + ostracods). After testing the detailed vertical distribution of living individuals
164 for three representative samples, showing significant numbers of living individuals within the
165 upper 3 cm, these were combined for microfaunal investigation and the lower 2 cm were
166 discarded.

167 Samples for sedimentological and geochemical analyses were dried at 40 °C and
168 carefully pestled by hand. For grain-size analysis, carbonates were dissolved with
169 hydrochloric acid (HCl; 10%) and organic matter removed using hydrogen peroxide (H₂O₂;
170 15%). In order to prevent aggregation, samples were treated with sodium pyrophosphate
171 (Na₄P₂O₇; 46 g/l). The grain-size distribution was determined on the <2 mm fraction using a
172 laser particle size analyser (Beckman Coulter LS 13320) with a laser beam (780 nm) applying
173 the Fraunhofer optical mode (Eshel et al., 2004). Since different species of Foraminifera and
174 Ostracoda often prefer different substrates (cf. Frenzel et al., 2010), the microfaunal
175 associations can be related to grain-size distribution.

176 The organic content was determined by measuring the concentration of total organic
177 carbon (TOC, constituting c. 50% of organic matter). This was accomplished using an
178 elemental analyser (elementar, Vario EL Cube), which enabled simultaneous measurements
179 of nitrogen (N) and the determination of total inorganic carbon (TIC). The derived C/N ratio
180 can provide information about the aquatic or terrestrial origin of organic matter (cf. Last &
181 Smol, 2001).

182 The salinity was measured under laboratory conditions using a conductivity meter
183 CO310 (VWR). Since the measurement was conducted with a delay of several months, the
184 results are expected to be influenced by evaporation within the closed vessels. However, this
185 should be consistent between all samples, so a general trend can be inferred.

186 ***3.3 Data processing***

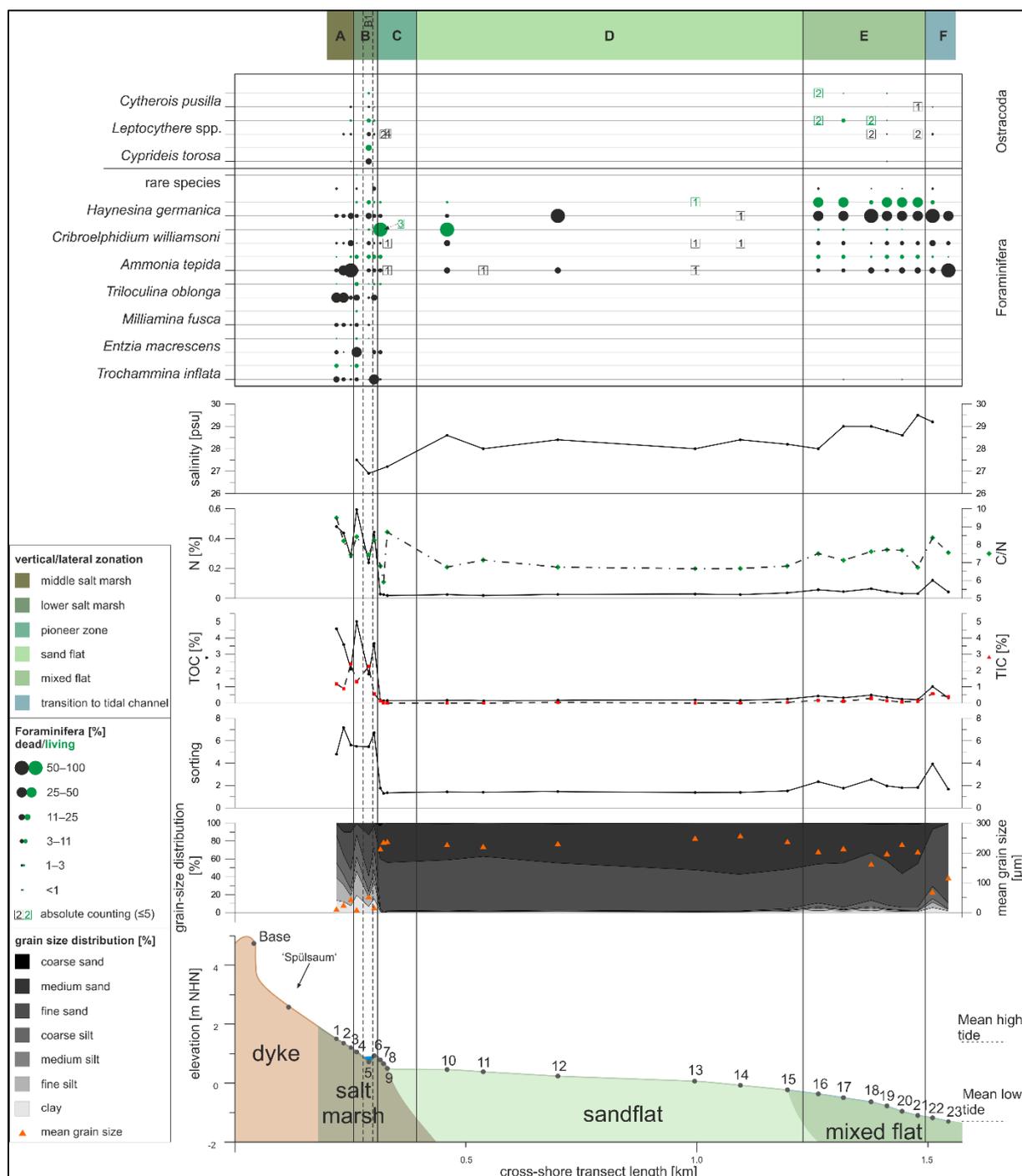
187 The calculation of univariate statistical grain-size measures after Folk & Ward (1957) was
188 carried out using GRADISTAT software (Blott & Pye, 2001). As preparation of the data set
189 for multivariate analyses, Pearson correlation coefficients were calculated between the
190 environmental parameters (sand amount, mean grain size, TOC, TIC, N, C/N, elevation) and
191 microfaunal data in order to detect possible auto-correlations. The distributions of foraminifer
192 and ostracod taxa as well as standardised environmental parameters were analysed by means
193 of multivariate statistics (PCA, CCA, DCA) in order to evaluate driving environmental
194 parameters and test whether species show unimodal or linear response along the main
195 environmental gradient. Both correlation and multivariate statistics were performed using the
196 software PAST (v. 3.21; Hammer et al., 2001). Afterwards, the TF was developed from the
197 training data using the software C2 (v. 1.7.7; Juggins, 2007). According to the gradient length
198 revealed by the DCA (3.3 standard deviation [SD]), a more unimodal species-environment
199 relation can be expected (Birks, 1995; Lepš & Šmilauer, 2003), wherefore modelling was
200 conducted using the weighted averaging-partial least squares (WA-PLS) method. To avoid
201 overfitting, a maximum of three components was modelled (cf. Kemp & Telford, 2015).
202 Bootstrapping cross-validation (1000 cycles) was used to evaluate the TF performance based
203 on the coefficient of determination (R^2_{boot}), providing an estimation of the grade of the linear
204 relationship between observed and estimated elevations in the training set, and the root mean
205 squared error of prediction (RMSEP), enabling the evaluation of the general predictive
206 capability of the TF (Milker et al., 2017). The most appropriate of the three modelled
207 components was chosen based on the lowest RMSEP and highest R^2_{Boot} . Visual presentation

208 of the data was accomplished by means of the software Grapher (v. 8.0.278) and the drawing
209 application CorelDRAW X8 (v.18.1.0.690).

210 **4 Results of microfaunal, sedimentological and geochemical investigations**

211 *4.1 Vertical and lateral zonation*

212 The investigated transect reaches from 53°45'42.27'' N, 7°43'27.76'' E (1.51 m NHN [m
213 above *Normalhöhennull* = standard elevation zero referring to gauge Amsterdam]) in the
214 north to 53°45'2.32'' N, 7°43'23.49'' E (-1.31 m NHN) in the south. The separation of six
215 zones (Zones A–F) was carried out based on qualitative interpretation of sedimentary (in
216 particular grain-size distribution, TOC) and microfaunal (in particular foraminiferal
217 abundance and composition) data in combination with field observations (Figs. 3, S1 [online
218 supplement]). Zone boundaries were defined in between two samples by considering the mean
219 elevation between them. Foraminifer and ostracod species are always mentioned in ranking
220 order concerning their abundances. In total, eight foraminifer and three ostracod taxa (see
221 Plate 1) were identified in both living and dead fauna. In general, much less living than dead
222 individuals occur and microfaunal densities vary strongly between zero and 2500 ind./10 cm³
223 (individuals per 10 cm³) throughout the transect.



224

225 **Figure 3.** Results of the investigated surface transect. From the bottom to the top: elevation profile
 226 with sampling points and landscape units observed in the field; grain-size distribution and mean grain
 227 size; sorting of the sediments; content of organic (TOC) and inorganic (TIC) carbon; Nitrogen (N)
 228 content and ratio of organic carbon and nitrogen (C/N); salinity trend measured for sampling points
 229 with present water coverage; foraminifer and ostracod species association; identified lateral and
 230 vertical zones (for vertical depiction see Fig. S1 [online supplement]).

231 Zone A (middle salt marsh), comprising the northernmost three samples (c. 1.51–
 232 1.13 m NHN; samples 1, 2 and 3) is characterised by very poorly sorted sandy mud in the
 233 upper and muddy sand in the lower part. The vegetation is characterised by *Limonium vulgare*

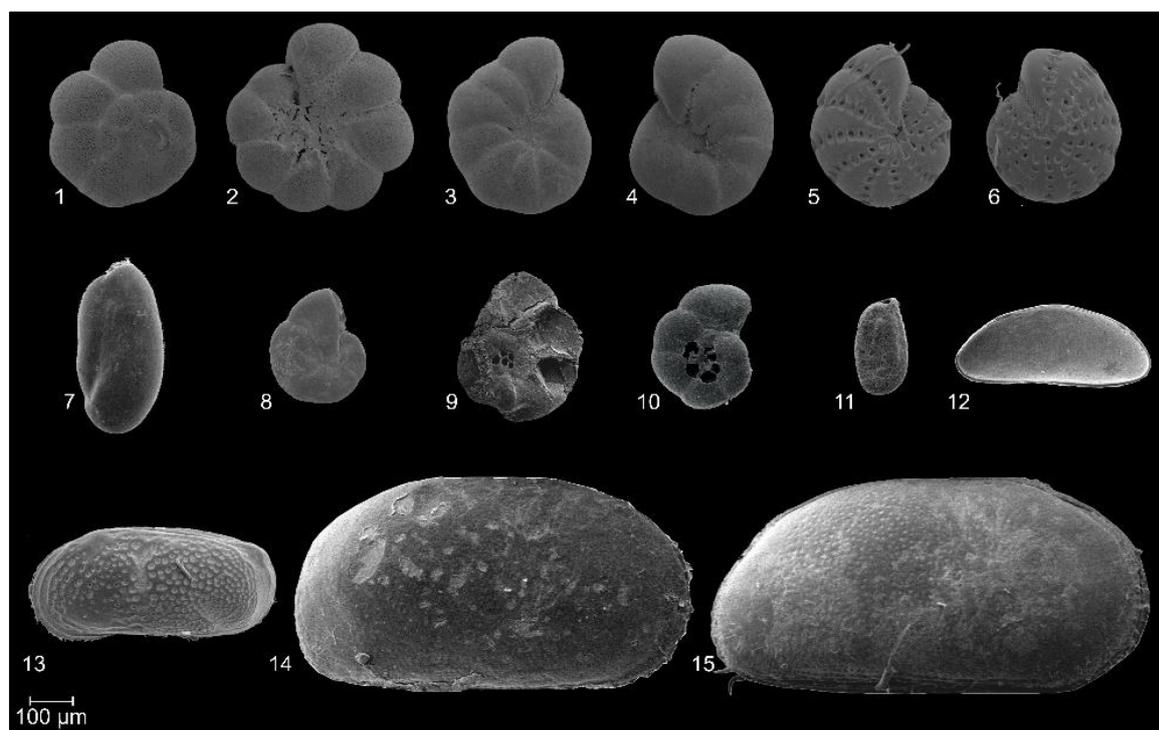
234 (sea lavender) and *Puccinellia maritima* (andel grass). TOC and TIC values show opposite
235 trends with TOC decreasing and TIC increasing towards lower elevations. The N content and
236 the C/N ratio both decrease towards lower elevations. No water cover was present. The
237 microfaunal composition is characterised by high diversity and high abundance (up to c. 2200
238 individuals/10 cm³). Foraminifers are dominated by *Triloculina oblonga* (Montagu, 1803) in
239 the upper and *Ammonia tepida* (Cushman, 1926) in the lower part followed by *Haynesina*
240 *germanica* (Ehrenberg, 1840), *Cribrulphidium williamsoni* (Haynes, 1973) and the
241 agglutinated species *Trochammina inflata* (Montagu, 1803), *Miliamina fusca* (Brady, 1870)
242 and *Entzia macrescens* (Brady, 1870). A few individuals of *Spirillina* sp. could also be
243 observed. Ostracods are dominated by *Leptocythere* spp., represented by *L. pellucida* (Baird,
244 1850), *L. castanea* (Sars, 1866) and *L. lacertosa* (Hirschmann, 1912), followed by *Cytherois*
245 *pusilla* (Sars, 1928) and *Cyprideis torosa* (Jones, 1850). However, ostracods show a much
246 lower abundance than foraminifers. Living individuals are barely present. The microfaunal
247 concentration increases towards the following zone (Zone B) from c. 600 ind./10 cm³ in the
248 uppermost sample (1) to c. 2300 ind./10 cm³ in the lowest sample (3). Most shells seem to be
249 well preserved (transparent) and only a few show slight signs of degradation (opaque/white
250 colour). Only *E. macrescens* repeatedly exhibits collapsed chambers, which could have
251 happened during sample treatment or after drying of the individuals or even prior to sampling
252 due to their very lightly agglutinated tests (e.g. Murray, 2006; Filipescu & Kaminski, 2011).

253 Zone B (lower salt marsh), comprising three adjacent samples (c. 1.06–0.86 m NHN;
254 samples 4, 5 and 6), is characterised by very poorly sorted sandy mud with an increasing sand
255 amount towards lower elevations. The vegetation is composed of *Atriplex portulacoides* (salt
256 bush), *Puccinellia maritima* (andel grass) and *Spartina anglica* (cord grass). The highest TOC
257 and second highest TIC values of the whole transect occur in this zone as well as the highest
258 values for N. Water coverage is partially given by small pools near the sampling points with a
259 salinity of 27.5 psu in the upper part of Zone B. This zone, with abundances of up to c. 600

260 individuals/10 cm³, is further defined by the presence of *T. inflata*, *E. macrescens* and *M.*
261 *fusca*. *E. macrescens* dominates the upper part (sample 20) while *T. inflata* dominates the
262 lower part (sample 5), both followed by the hyaline foraminifer species *T. oblonga*. *A. tepida*,
263 *H. germanica* and *C. williamsoni*. Ostracods are only present in the lower part of the zone,
264 dominated by *Leptocythere* spp. and accompanied by *C. pusilla*. Only ~11–22% of all present
265 foraminifers, but half of the ostracods were identified as ‘living’. However, compared to the
266 amount of foraminifers, ostracods only show very low abundances. Sample 5 taken from a
267 small salt-marsh pool (0.72 m NHN) stands out in Zone B and represents Subzone B1. It is
268 characterised by a much higher sand amount (sandy mud), higher TIC, lower TOC and N
269 values as well as a lower C/N ratio than in the rest of Zone B. The salinity also decreases to
270 the lowest value of the complete transect. The microfaunal composition changes in this sub-
271 zone with a slightly higher amount of living Foraminifera (~25%). Foraminifera are
272 dominated by *H. germanica* followed by *A. tepida* and *C. williamsoni*, accompanied by only a
273 few individuals of *T. oblonga* and only one specimen of *T. inflata*. Ostracoda are strongly
274 dominated by dead (~25%) and living (~43%) individuals of *C. torosa*, accompanied by
275 *Leptocythere* and *C. pusilla*. This sample shows the highest amount of ostracods throughout
276 the complete transect. Within the complete zone (including B1), the microfaunal
277 concentration decreases towards the next zone from c. 500 ind./10 cm³ to c. 100 ind./cm³.
278 Only very few shells seem slightly degraded, whereas the major part is well preserved.

279 Zone C (pioneer zone; c. 0.86–0.48 m NHN) comprises three samples (7, 8 and 9) and
280 represents a transition to Zone D, i.e. a transition from the salt marsh to the tidal flat. It is
281 characterised by moderately to well sorted sand. *Spartina anglica* (cord grass) dominates the
282 vegetation of this zone. No TIC and almost no TOC and N were documented. The C/N ratio
283 first decreases before increasing to the highest value throughout the transect in the last sample
284 of this zone. Water coverage in this zone occurred mainly in the lower part, which is the
285 border between salt marsh and sand flat, due to the neap tide situation at the sampling day in

286 2015. The salinity is higher than in Zone B. The amount of microfauna (mainly foraminifers)
 287 is much lower than in Zone B, even though the uppermost sample still shows a moderate
 288 concentration of individuals. It is strongly dominated (62%) by living individuals of *C.*
 289 *williamsoni* followed by *H. germanica* and *A. tepida* accompanied by only one individual
 290 each of *T. inflata* and *T. oblonga*. In terms of Ostracoda, only six individuals of *Leptocythere*
 291 occurred in the lower two samples. The microfaunal concentration strongly decreases with
 292 decreasing elevation with c. 120 ind./10 cm³ in the upper sample (7) and only 4–6 ind./10 cm³
 293 in the lower two samples. Most of the shells are well preserved and only very few seem
 294 slightly degraded.



295
 296 **Plate 1.** SEM images of frequently documented foraminifer (1–11) and ostracod (12–15) species. 1, 2:
 297 *Ammonia tepida* (Cushman, 1926); 3, 4: *Haynesina germanica* (Ehrenberg, 1840); 5, 6:
 298 *Criboelphidium williamsoni* (Haynes, 1973); 7: *Triloculina oblonga* (Montagu, 1803); 8, 9: *Entzia*
 299 *macrescens* (Brady, 1870); 10: *Trochammina inflata* (Montagu, 1803); 11: *Miliammina fusca* (Brady,
 300 1870); 12: *Cytherois pusilla* (Sars, 1928); 13: *Leptocythere pellucida* (Baird, 1850); 14, 15: *Cyprideis*
 301 *torosa* (Jones, 1850).

302 Zone D (sand flat; c. 0.48–0.30 m NHN) comprises six samples (10–15) and is the
 303 widest zone of the transect with a length of ~750 m. It is characterised by moderately well to
 304 well sorted sand with a coarsening trend towards lower elevations (medium sand increasing

305 from c. 40 to c. 52%, fine sand decreasing from c. 51 to 38%). No vegetation was present in
306 2015 (winter), while occasional carpets of algae characterised the zone in 2017 (summer).
307 TIC values are negligible as well as the only slightly higher TOC and N values. The C/N ratio
308 is at a quite constant level (6–7). Water coverage occurred in the form of small puddles or
309 micro-channels in a higher number in 2015 than in 2017. All samples are situated within these
310 water-covered areas. The salinity shows an only slightly varying trend (0.6 psu). There are
311 very few foraminifers in this zone (0–30 ind./10 cm³), dominated by living *C. williamsoni* in
312 the upper part, where *A. tepida* is also present, and by dead *H. germanica* in the central part.
313 The lower part of the zone comprises even fewer individuals while ostracods are completely
314 absent. The few foraminifers observed in this zone show signs of degradation, except for the
315 living individuals of *C. williamsoni*, which are well preserved.

316 In Zone E (mixed flat; c. -0.30–1.14 m NHN), comprising six samples (16–21), silt
317 and clay reappear (Fig. 3). It is characterised by a poorly to moderately sorted muddy sand to
318 pure sand. No vegetation is present. In this zone, for the first time, occasional molluscs induce
319 slight bioturbation of the upper centimetres of the sediment. TIC, TOC, N and the C/N ratio
320 show slight variations compared to zone D. Water coverage occurred in the form of small
321 puddles or micro-channels and the salinity increases from the upper to the lower part by
322 1.5 psu, resulting in the highest value of the transect (29.5 psu). Besides the grain-size
323 distribution, the most striking change is the reappearance of microfauna with generally
324 increasing concentrations towards lower elevations (from c. 50 to c. 900 ind./10 cm³). It is
325 dominated by *H. germanica* (living and dead) followed by *A. tepida*, *C. williamsoni* and two
326 individuals of *T. inflata*. The highest abundance of ostracods (20 individuals) occurs in
327 sample 17 dominated by living *Leptocythere* (like in the rest of zone E). While *C. pusilla* and
328 *C. torosa* are also present, some juvenile ostracod individuals remain indeterminable (8 out of
329 49 in total). Preservation of shells is mainly good and only very few individuals seem slightly
330 degraded.

331 Zone F (transition to tidal channel; c. -1.14 m NHN until at least -1.31 m NHN)
332 comprises two samples (22 and 23). With first increasing and then decreasing silt and clay
333 amounts, it is characterised by poorly to moderately sorted muddy sand. In 2015, no
334 vegetation was present, while in 2017 algae remains were visible along the levee of the tidal
335 channel. Furthermore, the levee was characterised by many mollusc shells (see Fig. 2d). In the
336 upper sample, TIC, TOC and N show a slight increase of 0.09–0.8%, while the C/N ratio
337 increases by ~1.6 and only the salinity shows a slight decrease of 0.3 psu. In the lower sample
338 23, all values are more similar to zone E. Due to the lack of water cover, no salinity was
339 measured for the lowest sample, but the salinity of the shallow water of the adjacent tidal
340 channel was measured with 29.3 psu. The foraminiferal composition is similar to that of zone
341 E, although the amount of living individuals decreases with decreasing elevation, as does the
342 microfaunal concentration (from c. 2500 to c. 1000 individuals/10 cm³). Towards the
343 lowermost sample (23), a shift in the dominance between the two most abundant tidal flat
344 foraminifer species of the transect – *H. germanica* and *A. tepida* – is observed; *C. williamsoni*
345 occurs as well. Ostracods are only present in the upper sample represented by dead
346 *Leptocythere* and *C. pusilla*. Approximately half of the shells or tests are well preserved,
347 while the rest appears to be slightly degraded.

348 **5. Results of statistical analyses**

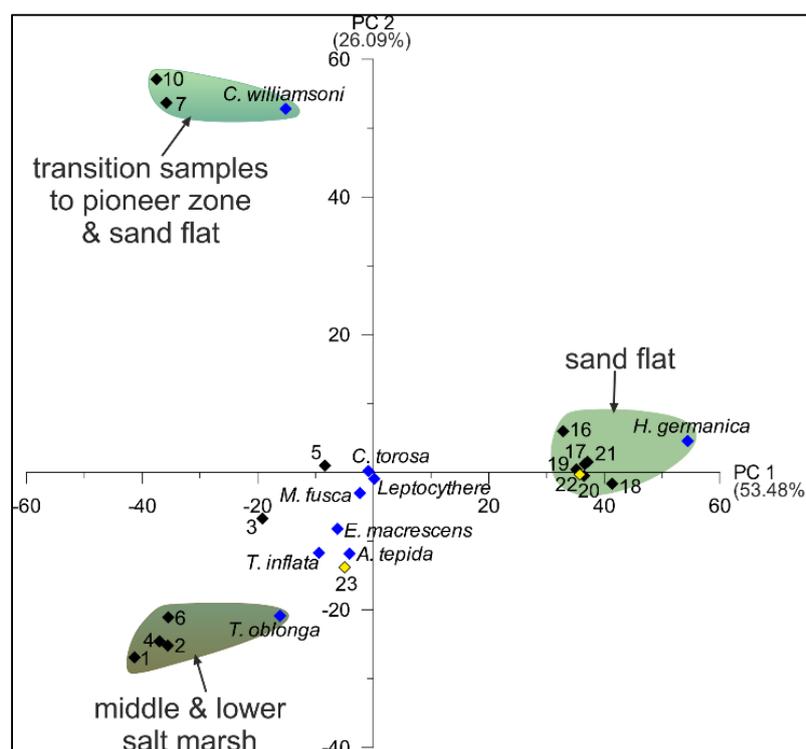
349 ***5.1 Driving environmental factors***

350 The Pearson correlation shows that *T. oblonga* is highly correlated with the sand amount, N
351 and TOC (and these factors are also highly correlated with each other). The sand amount and
352 the N content were therefore excluded for the downstream statistical analyses. Since TIC
353 seems to be rather insignificant throughout the transect and TOC is also connected to the grain
354 size, we also excluded TIC for the multivariate statistics. Furthermore, *Spirillina* sp. is highly
355 correlated with *M. fusca*, the latter being slightly more frequent. Therefore, the rare *Spirillina*
356 sp. was also excluded. In order to find variables, which account for as much of the variance in

357 our dataset as possible (cf. Davis, 1986; Harper, 1999), a principle component analysis (PCA)
358 was performed. In order to receive statistically relevant results, only samples with a minimum
359 of 40 individuals counted were considered, thus excluding almost all sand flat samples
360 between c. 0.39 and -0.29 m NHN. The most relevant axes for our modern dataset are PC 1
361 and 2 (see biplot in Fig. 4).

362 PC 1, with an explained variance of 53.48%, contrasts *T. oblonga* and *C. williamsoni*
363 along with all agglutinated foraminifer species with *H. germanica*. This includes all salt
364 marsh and transitional samples on the negative and all tidal flat samples on the positive side
365 leading to the conclusion of PC 1 describing a ‘salt marsh versus tidal flat’ factor, which
366 could be related to the duration of water cover, i.e. the elevation. PC 2, describing a variance
367 of 26.09%, opposes mainly *T. oblonga* (associated with the salt marsh samples) and *C.*
368 *williamsoni* (associated with the transitional samples of the pioneer zone and sand flat). Since
369 *C. williamsoni* tolerates higher salinities than most salt marsh species (Murray, 2006), PC 2
370 could relate to the salinity, which does not seem to have much of an influence on the tidal flat
371 samples. The two samples of zone F (transition to the tidal channel; samples 22 and 23
372 marked in yellow in Fig. 4) seem to be ‘misplaced’ by the PCA, since sample 22 is associated
373 with the tidal flat group, whereas sample 23 is situated at the ‘salt marsh’ side of PC 1 and
374 associated to *A. tepida*. This may be explained by the position at the margin of the tidal

375 channel and related higher-dynamic conditions, to which *A. tepida* seems to be better adapted.

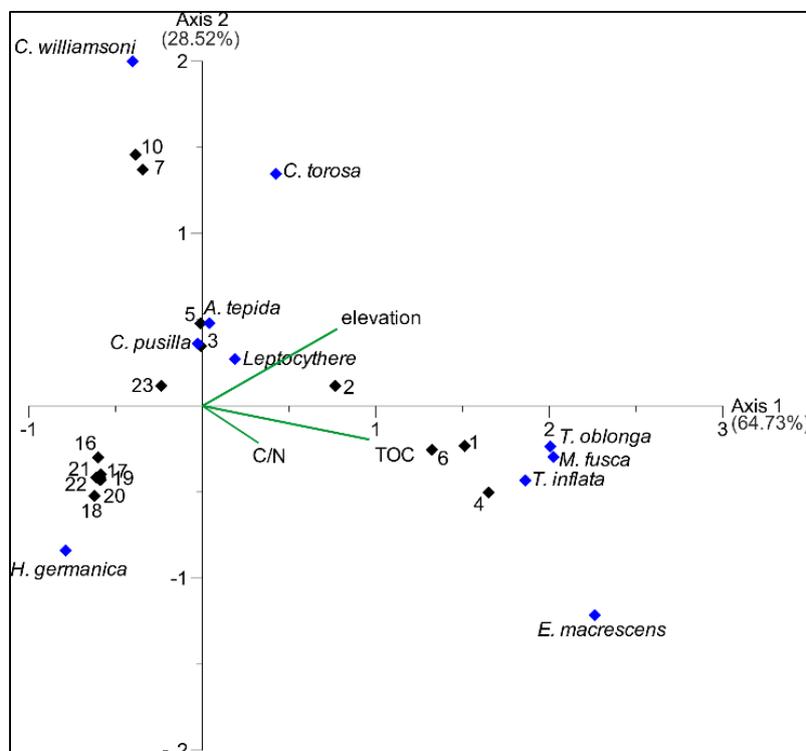


376

377 **Figure 4.** PCA biplots of the investigated surface transect with identified groupings (for colour legend
 378 of facies zones see fig. 3). Black diamonds represent samples (two outliers marked in yellow), blue
 379 diamonds microfaunal taxa.

380 As shown by the PCA, the elevation seems to have a strong influence on foraminifer
 381 and ostracod distribution. In order to test if it is the main driving environmental factor, a
 382 canonical correspondence analysis (CCA) was carried out including the microfaunal data and
 383 the remaining parameters elevation, TOC and C/N. The CCA biplot (Fig. 5) shows the first
 384 axis, describing a variance of 63.73%, with highest scores for TOC and elevation (in ranking
 385 order). The latter exhibits the highest score for the second axis, which describes a variance of
 386 28.52%. The C/N ratio seems rather irrelevant for both axes with the lowest scores for both.
 387 The different species exhibit different relations to the depicted environmental parameters.
 388 Since the second axis is mainly described by the elevation, the foraminifer species *A. tepida*
 389 and *C. williamsoni* and all three ostracod species show the highest relation to this parameter,
 390 whereas the salt marsh foraminifers *T. oblonga*, *M. fusca* and *T. inflata* are highly related to
 391 TOC, mainly describing the first axis. This indicates that the foraminifer and ostracod
 392 distribution is mainly influenced by the organic content and the inundation frequency related

393 to elevation. Since the elevation is related to both axes and the TOC content shows quite high
 394 correlation values concerning the elevation (~ 0.75), a strong influence of the elevation, related
 395 to water depth and inundation frequency, can be assumed.



396
 397 **Figure 5.** CCA biplot of the investigated surface transect. Black diamonds represent samples, blue
 398 diamonds microfaunal taxa. The three remaining environmental factors (elevation, TOC and C/N) are
 399 visualised by green lines. TOC and elevation have the highest scores for axes 1 and 2, identifying
 400 them as the main influence on the dataset.

401 A detrended correspondence analysis (DCA) was carried out in order to test the
 402 species-environment relationship. Since PCA and CCA confirmed the elevation (i.e.
 403 inundation frequency) as the strongest driving factor, we included only the elevation and the
 404 microfaunal data for the DCA. As the DCA plot (cf. Fig. S2, online supplement) shows, the
 405 length of the environmental gradient was determined as 3.3 SD, which indicates a rather
 406 unimodal species response (cf. Birks, 1995; Lepš & Šmilauer, 2003).

407 **5.2 Transfer function (TF) development and testing**

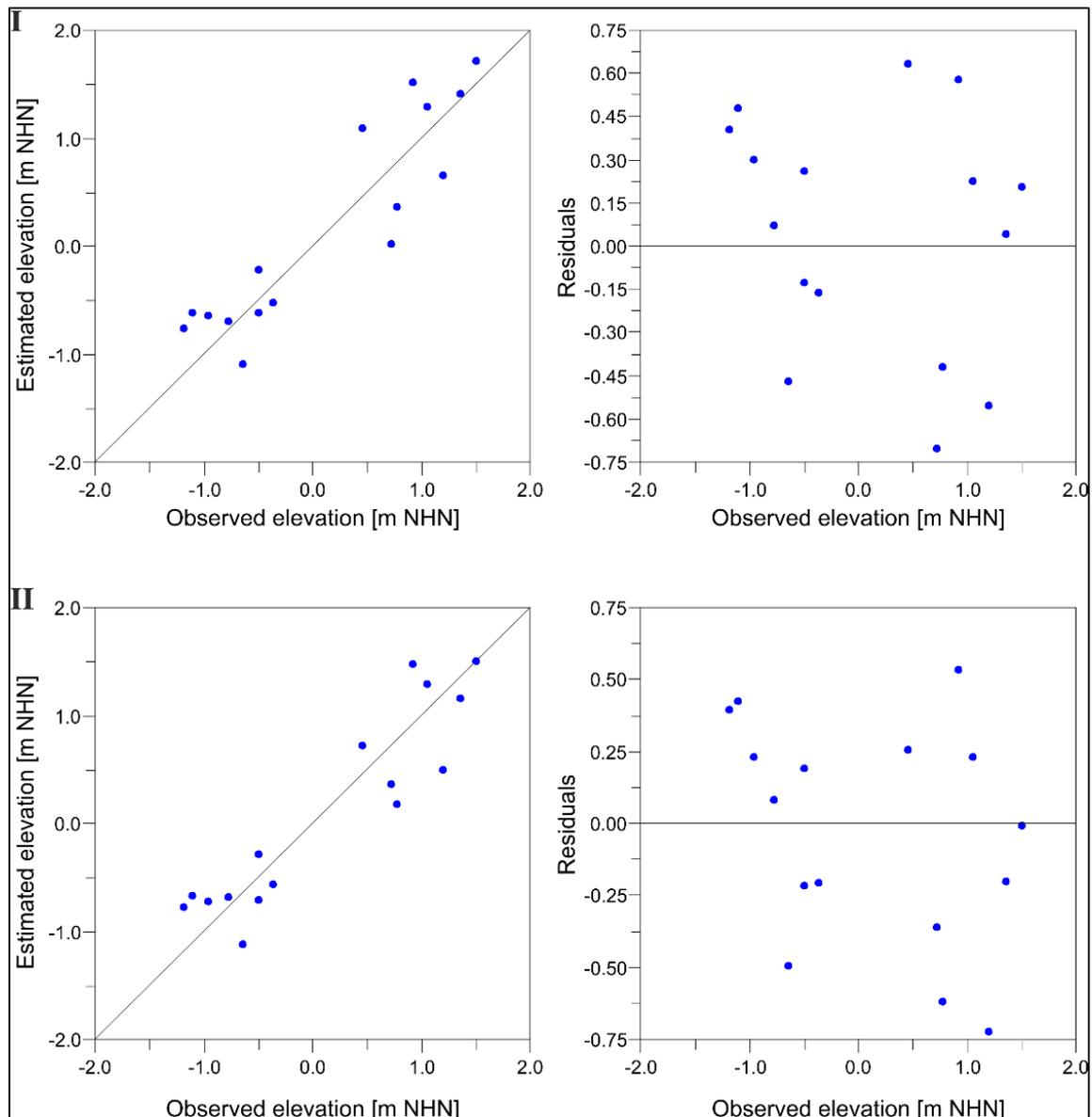
408 Since living associations of foraminifers and ostracods can be affected by seasonal differences
 409 and the 2015 and 2017 samples were taken during different seasons – in fact showing
 410 differences in the densities of living individuals (cf. Fig. 3) – only the dead assemblages were

411 used for the TF development. Those represent a result of habitat preferences and connected
412 taphonomic changes averaged over several years (e.g. Murray, 2000).

413 Two different models were developed for the TF (see Fig. 6): model I using
414 exclusively foraminifers, representing the most commonly applied procedure, and model II
415 including the ostracods. Again, only samples with a minimum of 40 individuals were
416 considered. For both models, component 2 seems to be the most suitable (lowest RMSEP and
417 highest R^2) and is presented here. Since during the initial modelling, sample 23, once again,
418 turned out to be an outlier, it was excluded from the dataset reducing the investigated
419 elevation gradient to a vertical distance of 2.69 m (+1.51 to -1.18 m NHN). Since samples
420 were taken during different tidal situations (neap and spring tide), the description of the
421 RMSEP is related to the mean tidal range instead of the mean spring tidal range.

422 Model I shows an R^2_{boot} of 0.82 and an RMSEP of 54.2 cm, which accounts for 20.2%
423 of the elevation gradient (and 20.1% of the mean tidal range). There is no visible trend of the
424 TF over- or underestimating samples in relation to their observed elevation and structures of
425 residuals are also not noticeable (Fig. 6).

426 Model II shows a slightly better R^2_{boot} of 0.84 and with 49.1 cm also a better RMSEP
427 accounting for only 18.3% of the total elevation gradient (and 18.2% of the mean tidal range).
428 Again, there is neither a clear trend of over- or underestimation related to the observed
429 elevation nor visible structures of the residuals (Fig. 6).



430

431 **Figure 6.** Results of testing the transfer function (TF) by bootstrapping cross validation (1000 cycles).
 432 Diagrams depict estimated vs. observed elevation (left diagrams) and deviation of each sample from
 433 the observed elevation (right diagrams) for both model I based on dead Foraminifera alone (top) and
 434 model II based on dead Foraminifera and Ostracoda combined (bottom).

435 **6 Discussion and evaluation of the modern training set**

436 **6.1 General observations**

437 In general, higher amounts of fine-grained sediments, TIC, TOC and N correlate very well with
 438 the presence of microfauna, whereas areas of coarser-grained sediments and constantly low
 439 TIC, TOC and N contents correspond to areas of low abundance or even complete absence. The
 440 C/N ratio, lying between 4 and 10 throughout the complete transect, indicates that all organic
 441 matter originates from aquatic sources (cf. Last & Smol, 2001). In accordance with our

442 expectations, the salinity shows a general rising trend from the salt marsh to the tidal channel
443 and increasing water cover and depths (cf. Kaiser & Niemeyer, 1999; Flöser et al., 2011).

444 **6.2 Living vs. dead fauna**

445 Comparing the living and dead associations we notice differences along the transect. The
446 remarkably lower percentages of living than dead individuals occurring in the middle salt
447 marsh (zone A) suggest a quite good preservation of tests without significant dissolution
448 effects. Furthermore, a part of the observed foraminifers and ostracods could be allochthonous
449 and introduced during spring tides or storm surges (cf. de Rijk & Troestra, 1999).

450 In the lower salt marsh (zone B), especially in the salt-marsh pool (subzone B1), the
451 discrepancy between living and dead individuals is smaller, indicating either a poorer
452 preservation of empty tests or better living conditions, mostly due to the higher frequency of
453 water coverage at this elevation. Moreover, the permanently covered salt-marsh pool provides
454 good living conditions with new, probably oxygen-rich water inundating during high tide and
455 provided by rainfall combined with bioturbation (roots) and diffusion (cf. de Rijk & Troestra,
456 1999; Berkeley et al., 2007). Furthermore, its surrounding is sheltered by the salt marsh plants
457 of the lower salt marsh enabling permanent water coverage, which results in the quite high
458 number of living foraminifers and ostracods, especially *C. torosa* (e.g. Athersuch et al., 1989;
459 Murray, 2006). Probably, a combination of better living conditions (higher numbers of living
460 individuals) and poorer preservation led to the observations for this zone.

461 In the pioneer zone (zone C), a clear dominance of living *C. williamsoni* is observed,
462 whereas the dead fauna is more diverse. Since *C. williamsoni* prefers sediments with <60%
463 mud/silt content (Murray, 2006), this pattern correlates well with the abruptly increased sand
464 amount in this zone, also reflecting the higher dynamics in the transition area between salt
465 marsh and tidal flat (cf. Nyandwi & Flemming, 1995). Due to a higher energy level, dead
466 individuals could, once again, be introduced by the tidal current. The situation is similar in the
467 upper part of the sand flat (zone D), where the transition sample again is strongly dominated

468 by living *C. williamsoni*. However, since the rest of the sand flat shows only one living and a
469 few dead individuals, dynamics seem to get too intense towards the lower parts of the sand
470 flat for the survival of foraminifers or tests underlie *post-mortem* removal by currents
471 (Hofker, 1977). Another reason for the very low occurrence of microfauna may be the very
472 low (organic and inorganic) carbon content in the sand flat. Processes of early diagenesis (cf.
473 Berkeley et al., 2007) could influence the test preservation through changed saturation rates of
474 calcium carbonate (CaCO_3) causing the dissolution of tests (Sanders, 2003).

475 A completely different situation is documented in the mixed flat (zone E).
476 Foraminifers show a similar pattern in both living and dead associations indicating a good
477 fossilisation potential (cf. Smith, 1987). Ostracods show higher abundances of living
478 individuals in the upper and of dead ones in the lower part suggesting that they experience
479 *post-mortem* transport towards the tidal channel (cf. Edwards & Horton, 2000; Frenzel &
480 Boomer, 2005). In the transition area to the tidal channel (zone F), living individuals are very
481 few compared to dead ones, which may be due to the current of the channel complicating the
482 settlement of foraminifers as well as ostracods (cf. Hofker, 1977; Murray, 2006). However,
483 since dead shells are easier to be carried away by the current, this could again suggest a very
484 good preservation of empty tests. Still, it needs to be taken into account that a certain part of
485 the observed dead individuals is probably introduced by the tidal current. The few dead
486 ostracods could have been transported from the adjacent mixed flat.

487 **6.3 Evaluation of the transfer function (TF)**

488 Adding the ostracod data to our training set improves sea-level estimations for the
489 higher elevation stations only. The reason for this result is the higher abundance of ostracods
490 in these samples from the tidal pond and surroundings. Thus, more detailed data would likely
491 improve the performance of the transfer function. We would expect a similar outcome for the
492 deeper stations as well but this needs samples with higher ostracod counts, a target for future
493 studies.

494 Although the inclusion of ostracods clearly improves the TF performance and an
495 RMSEP of 18.3% seems acceptable (cf. Barlow et al., 2013), a vertical error of ~49 cm,
496 leading to a total error range of the indicative meaning of ~1 m, is still comparably large
497 (Edwards & Wright, 2015). Since other studies of similar environments focus only on the
498 vegetated marsh (e.g. Edwards & Horton, 2000; Gehrels & Newman, 2004; Kemp et al.,
499 2013; Müller-Navarra et al., 2017), the relatively high vertical error could be related to the
500 high environmental gradient (2.69 m; approx. the mean tidal range of Spiekeroog). However,
501 the tidal flat needs to be included in the TF, since the sediment cores dedicated to the future
502 TF application cover large sections of tidal flat and salt marsh deposits. In general, it has to be
503 noted that the exclusion of the sand-flat samples with <40 individuals leads to a lack of
504 information about estimates within the elevation range of these samples (from 0.39 to -0.29 m
505 NHN), which may lead to a deteriorated predictive ability for equivalent palaeo-elevations.
506 We expect that a higher number of training samples will result in a better TF performance as
507 most studies base their TF on a minimum of 40 samples, resulting in smaller error ranges (e.g.
508 Kemp et al., 2012; Müller-Navarra et al., 2016, 2017; Milker et al., 2017). In a next step we
509 will, therefore, increase the total number of samples in order to fill the elevation-gap created
510 by the weak sand flat samples.

511 ***6.4 Transfer function (TF) vs. peat-based reconstruction***

512 The vertical error range (~1 m) of model II of our TF is significantly smaller than the
513 one of existing peat-based RSL reconstructions of up to 3–5 m (e.g. Long, 2006; Bungenstock
514 & Schäfer, 2009; Bungenstock & Weerts, 2010, 2012; Baeteman et al., 2011). Reasons for the
515 better performance of the TF include:

516 The TF provides a direct relation to the sea level, whereas peat has an indirect relation
517 to the sea level. However, the indicative meaning of peat is still not universally defined (cf.
518 Baeteman, 1999; van de Plassche et al., 2005; Bungenstock & Schäfer, 2009; Wolters et al.,
519 2010). Moreover, basal peat cannot always be used as sea-level index point. For example, for

520 the early Holocene Wolters et al. (2010) document a basal peat, which cannot be linked to sea
521 level, as sea level was ~17 m lower, when peat growth started. They state that sea level
522 independent paludification in special topographic conditions is well known as described e.g.
523 by Jelgersma, 1961; Lange & Menke, 1967; Baeteman, 1999. However, widespread
524 intercalated peat layers are, in general, used as RSL index points, but close investigation of
525 formation processes is essential (Bungenstock & Schäfer, 2009; Bungenstock & Weerts,
526 2010).

527 Post-depositional compaction results in high uncertainty for peat-based RSL
528 reconstructions and significantly affects intercalated peats and the upper parts of basal peats.
529 Horton & Shennan (2009) found average compaction rates of 0.4 ± 0.3 mm/yr for peats buried
530 in Holocene sequences along the east coast of England. The TF, however can be applied to a
531 wide range of intertidal facies and sequences comprising large amounts of compaction-prone
532 peat can be avoided.

533 The microfossil-based TF also helps to avoid uncertainties imposed by relocated peat,
534 which is ripped off at peat cliffs in so-called ‘*Dargen*’ and transported over wide areas (e.g.,
535 Pliny the Elder, 77; Streif, 1990; Behre & Kuçan, 1999; van Dijk et al., 2019) potentially
536 resulting in age inversions in Holocene stratigraphies and invalid RSL indication.

537 Finally, the microfossil-based TF is a promising tool to derive RSL information from
538 the uppermost part of the Holocene sequence in the wider region covering the last 2000 years,
539 where peats are usually rare.

540 ***6.5 Method evaluation***

541 As a few additional samples were taken during the summer, whereas the main transect was
542 sampled during winter time, differences in the living microfauna between these samples could
543 be well explained by seasonal differences. However, since only dead individuals were used
544 for the TF development, in order to capture information over a longer time period (cf. Murray,
545 2000), this is not expected to influence the outcome of our study.

546 Concerning the sampling thickness, most studies dealing with microfaunal surface
547 distributions only use the uppermost 1 cm of the surface sediments (e.g. Kemp et al., 2012;
548 Korsun et al., 2014; Shaw et al., 2016; Müller-Navarra et al., 2016, 2017). However, due to
549 the high dynamics in the meso-tidal Wadden Sea and expected infaunal foraminifer taxa down
550 to a depth of up to 5 cm (Hofker, 1977), we decided for deeper sampling. By investigating
551 down to a depth of 3 cm, we account for most of the potential habitats of living individuals in
552 order to better represent the modern conditions in our analysis. Given the dm-scale accuracy
553 of the TF, the error imposed by the vertical integration of 3 cm is negligible for future RSL
554 reconstructions. This sampling depth will, however, require undisturbed fossil inter- and
555 supratidal layers with a minimum thickness of 3 cm for the future application of the TF.

556 Many of the studies applying Foraminifera to sea-level problems pick the individuals
557 wet in order to prevent drying of organic components and potential damaging of agglutinated
558 taxa (cf. de Rijk, 1995; Edwards & Wright, 2015; Milker et al., 2016; Müller-Navarra et al.,
559 2016, 2017), whereas in the present study most of the samples were picked dry. However,
560 since we did not observe any significant effects of drying on species associations or
561 preservation of agglutinated taxa, which is similar to observations of, e.g., Schönfeld et al.
562 (2013), we assess our results to be comparable with those of previous studies.

563 **7 Conclusion and outlook**

564 The investigated surface transect in the back-barrier salt marsh and tidal flat of the island of
565 Spiekeroog shows a clear vertical as well as lateral zonation of both foraminifers and
566 ostracods. While environmental factors like the hydro-energetic level (reflected by grain-size
567 distribution), the food availability (organic carbon) and the CaCO₃ saturation (inorganic
568 carbon) influence this zonation, the major influence is given through the water depth or the
569 duration of water cover (elevation relative to m.s.l.). Hence, our surface transect shows a good
570 potential for the establishment of a relative sea-level transfer function (RSL TF). The
571 common TF model, using only dead foraminifer associations, was improved by ~5 cm

572 (vertical error), resulting in an improvement of the error range of ~10 cm, by including dead
573 ostracod associations. The improved TF provides an R^2_{Boot} of 0.84 and a vertical error of
574 49.1 cm accounting for 18.3% of the investigated elevation gradient of ~2.7 m, which is the
575 approximate tidal range of Spiekeroog (BSH, 2018). Even though this vertical error is already
576 lower than the one associated with previously used sea-level index points such as basal or
577 intercalated peats, a clear demand for higher resolutions and lower error ranges remains (cf.
578 Vink et al., 2007; Bungenstock & Schäfer, 2009; Bungenstock & Weerts, 2010, 2012;
579 Baeteman et al., 2011). Thus, further improvements of our TF will be attempted in the near
580 future by integrating additional modern local samples in order to expand the modern training
581 set. Further improvements could probably be accomplished by narrowing the environmental
582 gradient or by combining the dataset with existing data from North Frisia collected by Müller-
583 Navarra et al. (2017) in order to develop a regional TF. In a final step, the RSL TF will be
584 applied to Holocene sedimentary records already recovered by the WASA (Wadden Sea
585 Archive) project (Bittmann, 2019).

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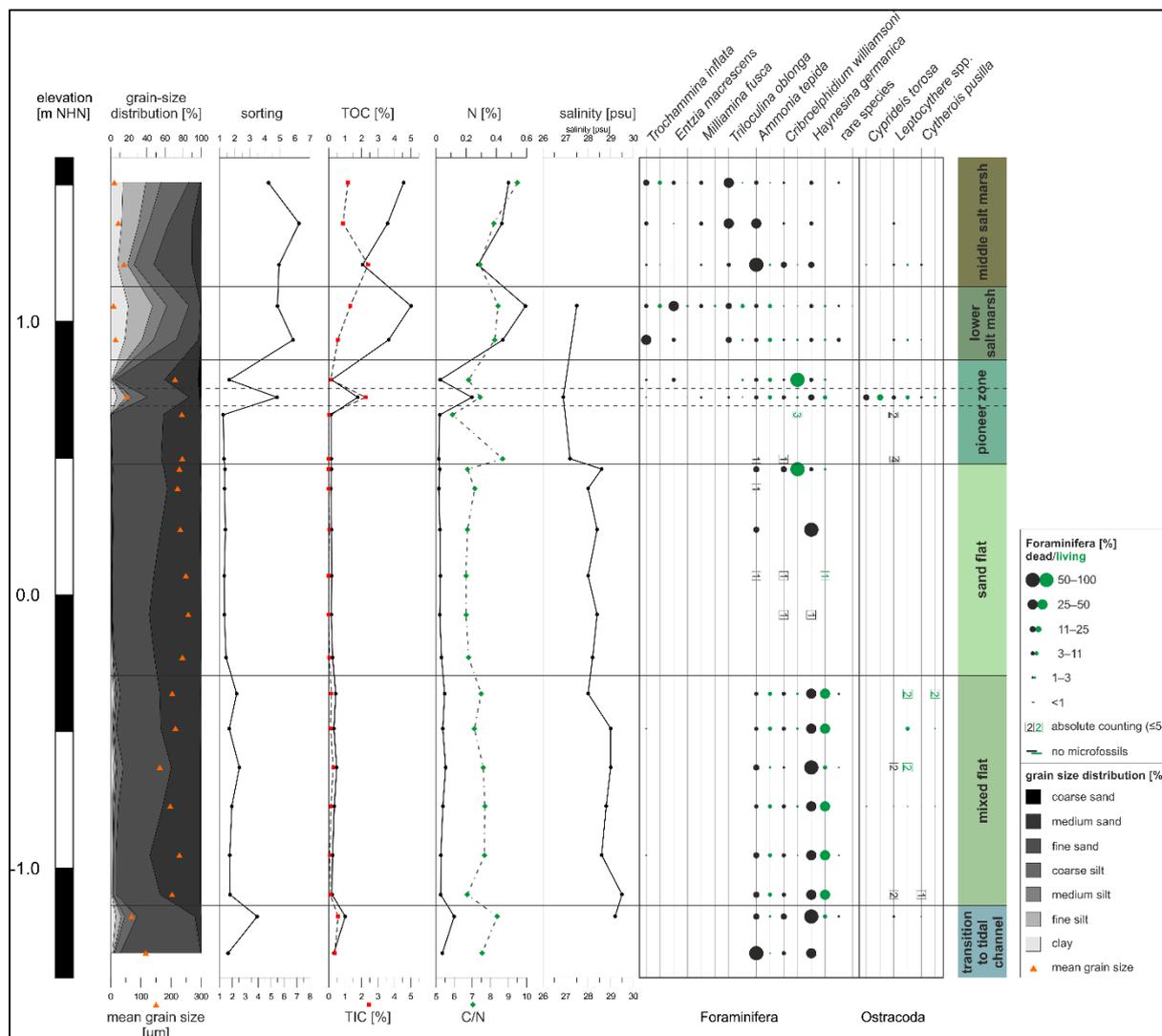
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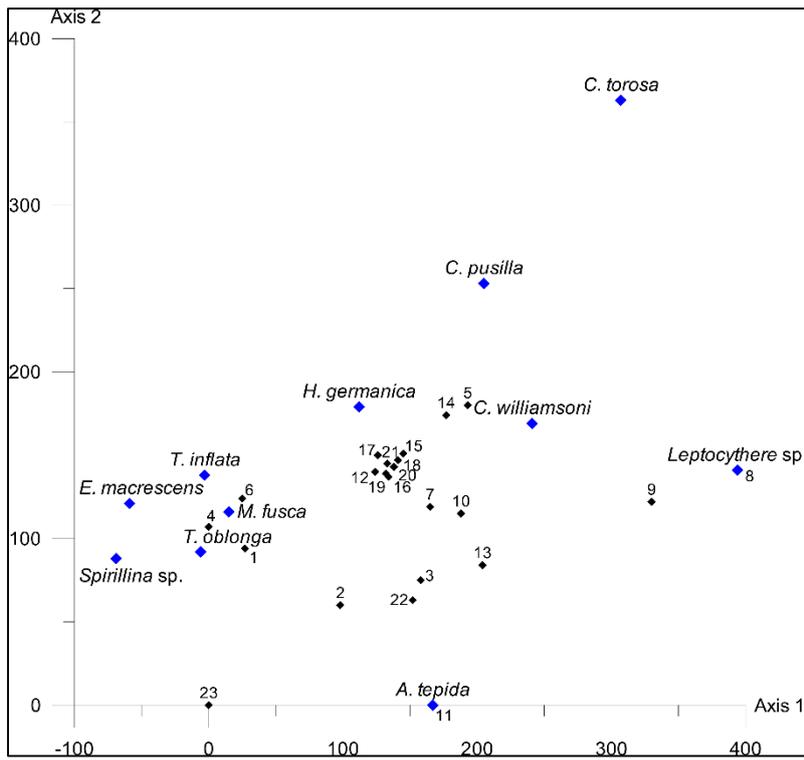
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851 **Supplementary material**



855

856 **Figure S 2.** DCA plot showing the length of the environmental gradient (x=330, i.e. 3.3 pointing to
 857 unimodal species distributions). Samples are represented by black, species by blue diamonds.

858