

Methods relieving comparison of living and death assemblages

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ABSTRACT: Living (LAs) and death assemblages (DAs) from the same samples (sites) can be compared based on total densities, species densities, species richness and heterogeneity (evenness). Preferably densities (standing crop), obtained by normalization of absolute frequencies to unit sample size, should be used to compare samples, especially for LAs. Combinations of the above four characteristics enable a better insight into the relations between LAs and DAs. The 'Incorporation Value' weighs the proportions of living individuals on total individual numbers with similarities in species composition between both assemblages, yielding the instantaneous integration grade of living individuals into the death assemblage. Diversity diagrams based on species richness (abscissa) and heterogeneities (ordinate), standardized over all investigated samples, simultaneously characterize differences in diversities. The standardized vector between LA and DA in the above-mentioned coordinate system characterizes differences in species richness and heterogeneity in a combined manner, where all coefficients of species richness and heterogeneities can be used.

Keywords: Density; similarity; diversity; species richness; heterogeneity

INTRODUCTION

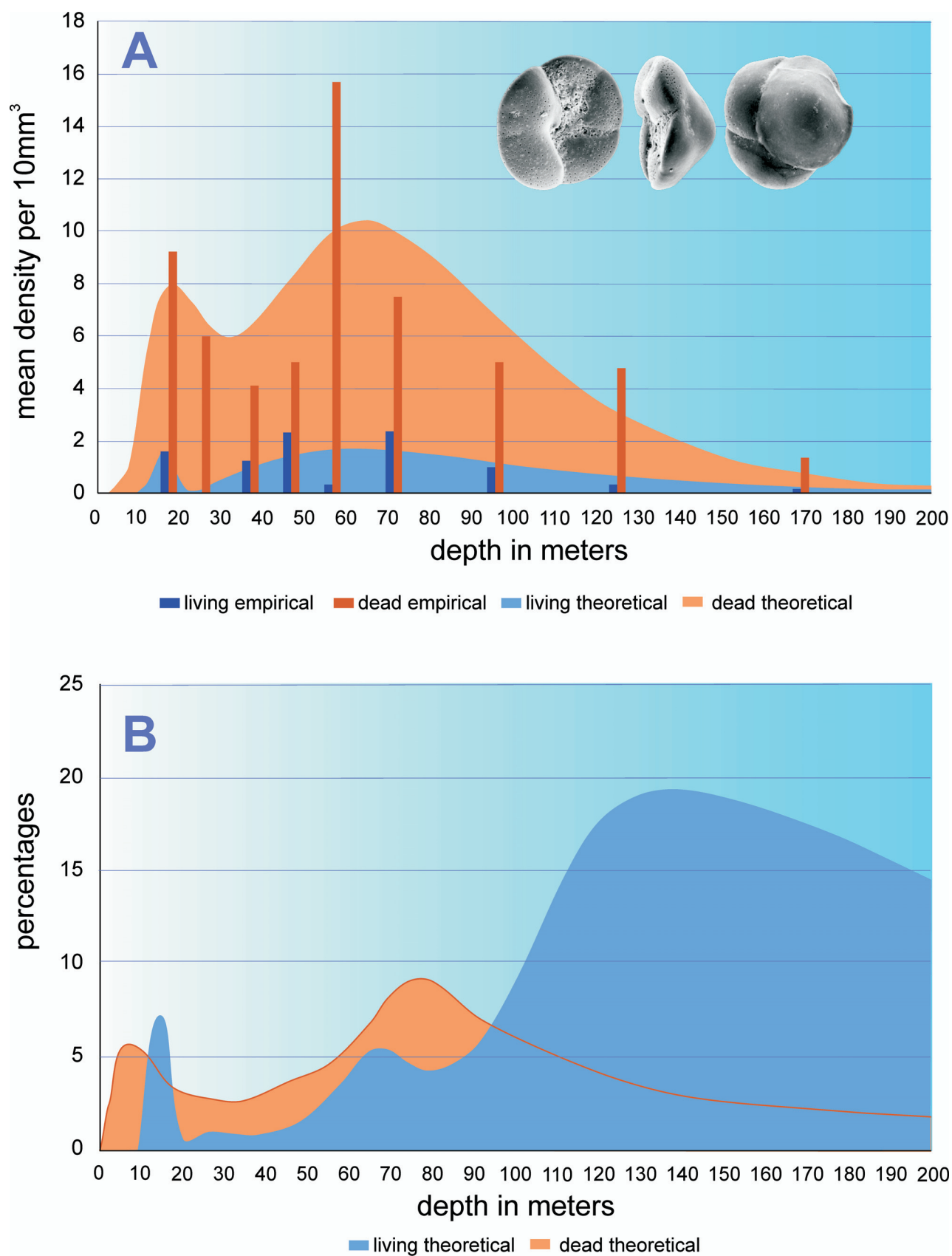
Relations between living (LA) and death assemblages (DA) are the key issue for estimating the influence of environmental and taphonomic factors on LAs and transforming these influences to DAs. Thus, relationships between LAs and DAs are important for estimating environmental factors in the fossil record, where DAs can be altered by various processes during fossilization and scaled up by temporal averaging and spatial transport (e.g., Kidwell and Flessa 1996, Martin 1999). Marine organisms with fossiliferous shells that are abundant on a macroscale, such as mollusks (e.g., Kidwell 2007), and on a microscale, such as foraminifera (e.g., Murray 1976), are the main objects of investigation because of their high fossilization potential and long geological history. Moreover, they occupy all marine benthic environments from the estuarine to the deep sea and from the poles to the equator.

Assemblages can be described in two ways: one is based on similarities in species densities, the other concentrates on differences in species diversities. A huge number of methods and indices have been developed for investigating similarities (e.g., Clifford and Stephenson 1975, Krebs 1999, Hammer 2016) and diversities (e.g., Magurran 2004, Magurran and McGill 2011).

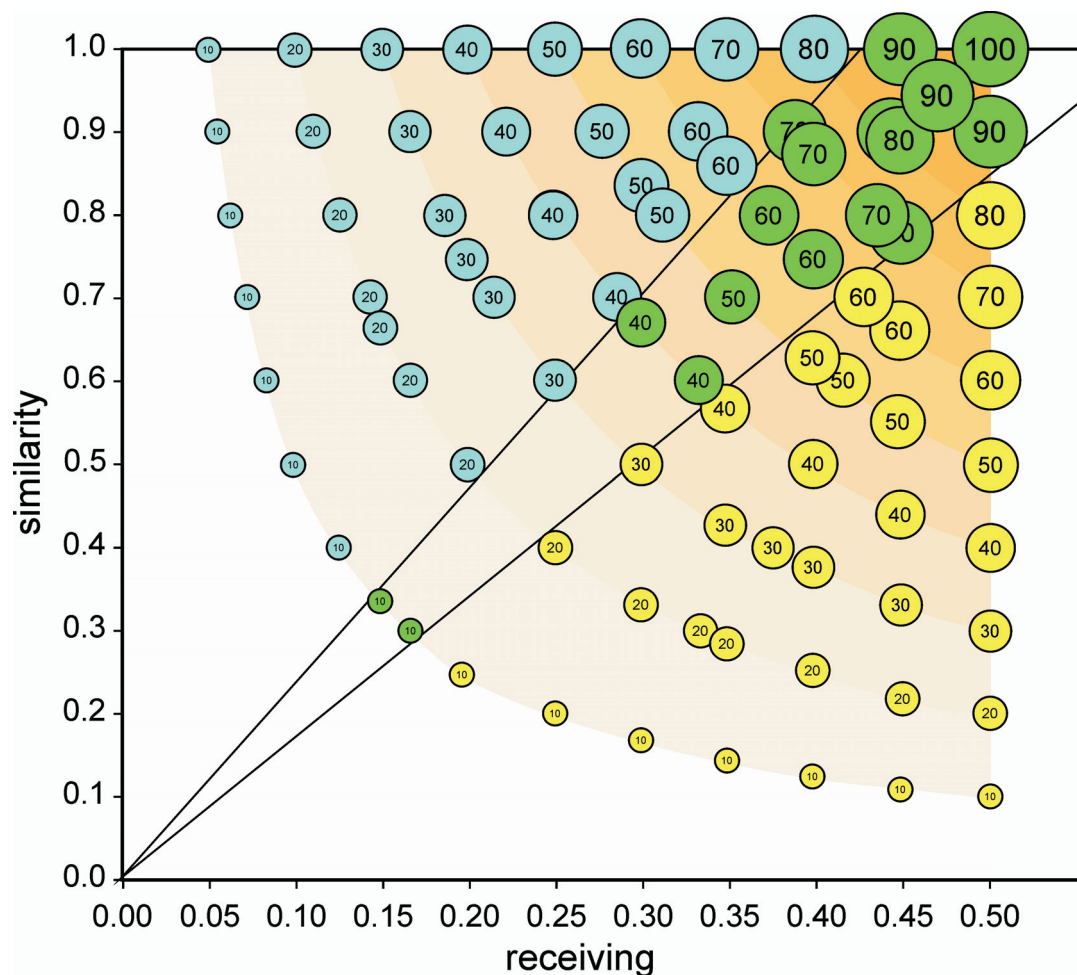
Parameter combinations enable direct comparisons between LAs and DAs expressed in a single index. 1) Differences in densities were measured based on the proportion of living individuals to the total number (living plus dead individuals) (Jorissen and Wittling 1999, Duros et al. 2014, Al-Dubai et al. 2017). 2) Simi-

larities in species composition between LAs and DAs were measured by the Chi-Square Statistic (Jorissen and Wittling 1999), Bray-Curtis Similarity (e.g., Diz and Francés 2009, Tomašových and Kidwell 2011), Renkonen Index (Duros et al. 2014) and Chao's Jaccard Index extended to abundance data (e.g., Kidwell 2007, Korpanty and Kelley 2014, Albano et al. 2016). 3) The disorder of ranks in species abundance were commonly expressed in Spearman's Rank Correlation Coefficient (Kidwell 2007, Schumacher et al. 2007, Albano et al. 2011, Weber and Zuschin 2013, Korpanty and Kelly 2014, Zuschin and Ebner 2015, Martins et al. 2016) or using the parameter R of the Analysis of Similarities ANOSIM (Zuschin and Stachowitsch 2007, Weber and Zuschin 2013). 4) Species richness is directly compared using two differences between species richness measures. First, the Values of Species Richness (Olszewski and Kidwell 2007) was used for mollusks (Albano and Sabelli 2011, Korpanty and Kelly 2014, Albano et al. 2016). Second, differences in Interspecific Encounter (Δ PIE) between DAs and LAs were introduced and used (Albano et al. 2016).

Like the comparison of densities over time intervals (Horton 1999), the diversity measures Species Richness, Heterogeneity and Evenness can simultaneously be compared over time intervals, which is named SHE Analysis. This analysis was performed on benthic foraminifera (Horton and Murray 2006, Wilson et al. 2017). A further method used for comparing LAs and DAs over spatial or temporal gradients is the nonparametric multivariate ANOVA (Anderson 2001, Tomašových and Kidwell 2011).



TEXT-FIGURE 1
Depth distribution of *Gavelinopsis praegei* offshore the Ria de Aveiro lagoon outlet (Portugal). (A) Densities of living and dead individuals. (B) Percentages of living and dead individuals. Data from Martins et al. (submitted).



TEXT-FIGURE 2

Incorporation Values pictured as circle areas in a diagram spanned by the ratio between densities of LAs and total densities (Receive) at the abscissa and the cosine between LAs and DAs (Similarity) at the ordinate. Blue circles indicate the dominance of similarities, yellow circles the main influence by proportions of living/total densities, while green circles depict balance.

In the following, indices and graphical methods are developed that may facilitate the interpretation of differences between LAs and DAs. Comparisons between commonly used and the new methods are based on foraminifera from the Ria de Aveiro lagoon outlet (Portugal) with 105 samples (Martins et al. 2018) and from shelf transects in front of the lagoon outlet based on 44 samples (Martins et al. submitted).

All complex analyses were done using the statistical program packages IBM SPSS Statistics 22 and PAST 3.12 (Hammer 2016), while the remaining calculations were performed in Excel (Microsoft Office 2016).

PARAMETERS DESCRIBING ASSEMBLAGES

Abundance of individuals per species within confined investigation areas, generally named quadrats in ecological research (Krebs 1999), characterizes assemblages. Abundance can be expressed by densities, biomass, or cover, the latter specifically for plants (Bonar et al. 2011).

Density

Densities are abundances normalized to unit quadrats (standing crop). They characterize the size and composition of assemblages in the comparison of LAs and DAs, where marine invertebrates with shells are preferably used. Sample quadrats can be either surface areas or sediment volumes, whereby the latter are important when investigating organisms on a microscale that live on (epifaunal) and/or within the sediment (infaunal).

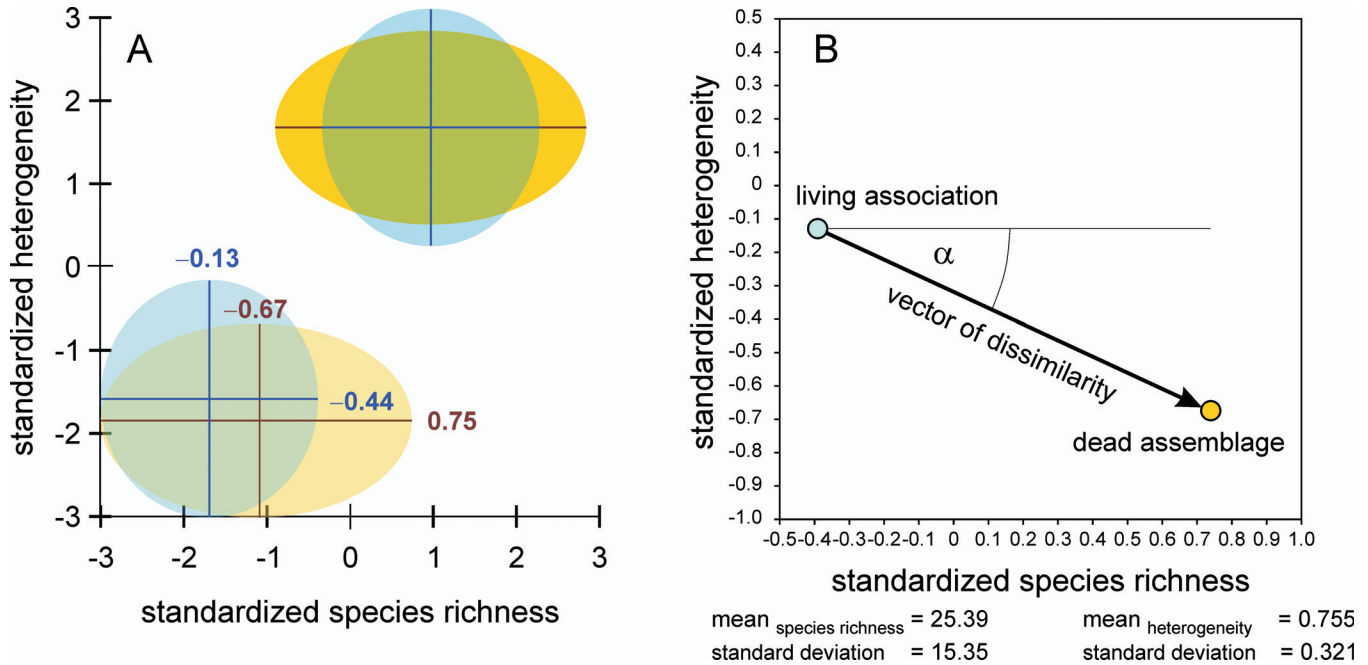
Two density measures are in use. First, the abundance n of individuals in a sample quadrat k normalized to units results in

$$\text{density}_k = \frac{\text{unit quadrat}}{\text{observed quadrat}_k} n_k \quad (\text{Eq. 1})$$

that represents the total density of the quadrat (Hammer et al. 2001). Species densities j within quadrat k are then defined by

$$\text{density}_{jk} = \frac{\text{unit quadrat}}{\text{observed quadrat}_k} n_{jk} \quad (\text{Eq. 2})$$

where j indicates the species (Hohenegger et al. 2014).



TEXT-FIGURE 3

Standardized diversities. (A) Diversity diagram of LA (blue) and DA (ochre) in the coordinate system of standardized species richness and heterogeneity. Lower left: graphical achievement of the standardized values for species richness (-0.391 for the LA, 0.739 for the DA) and heterogeneity (-0.159 for LAs, -0.674 for DAs) resulting in axes lengths for species richness of 2.609 (resulting from $-0.391 - (-3.000)$) for LA, 3.739 for DA, and due to heterogeneity of 2.841 for LA and 2.362 for DA. (B) Vector between LA and DA of site 128 (Martins et al. 2018, figs 1, 4) in the standardized coordinate system of species richness. The original means and standard deviations for diversity measures are given.

Particularly in gradient analyses, absolute species frequencies should be used to determine densities because proportions and percentages lose independence between species frequencies by $p_{jk} = n_{jk} / n_k$, thus proportions depend on the differing sample sizes n_k . Therefore, they cannot explain abundance trends of a single species along an environmental gradient, especially in living individuals but also in dead assemblages (text-fig. 1). This is not valid for community analyses along a gradient, where the use of percentages often leads to easier interpretations.

The stopping of counting at approximately 300 specimens in samples with an enormous number of individuals is commonly recommended in micropaleontological research (Patterson and Fishbein 1989, Murray 2006). This leads to incomparable species frequencies because 300 specimens are attained at different sample size, thus, similar to proportion and percentages, becoming incomparable to densities that are based on unit quadrats.

Therefore, normalization to unit quadrats completely reflects latent densities, while percentages and restricted counts do not affect diversity measurements, but can lead to inaccurate estimates of species frequencies along a gradient due to the interdependence of species by different quadrat size.

Diversity

Diversity is an equilibrium/disequilibrium measure of a biotic community and allows to understand the degree of dominance or competition among species living in a particular area. DAs'

diversity incorporates the relationship with living association and sedimentation (deposition or removal of tests) and other taphonomic effects such as dissolution.

Species diversity, in a broader sense (*s. lat.*), is divided into species richness and heterogeneity/evenness (Krebs 1999), whereby the latter is also termed diversity, but in a restricted (*s. str.*) sense (Mauerer and McGill 2011).

Species richness S of a quadrat (site, sample) counts the number of species j in an assemblage. To obtain species richness for the universal assemblage, using $n \rightarrow \infty$ leads to the expected species richness S_{max} (see Gotelli and Colwell 2011). This type of diversity disregards densities. Several methods of calculating species richness have been developed (Gotelli and Colwell 2011), whereby in foraminifera the most common approaches are the Margalef Index (Margalef 1968)

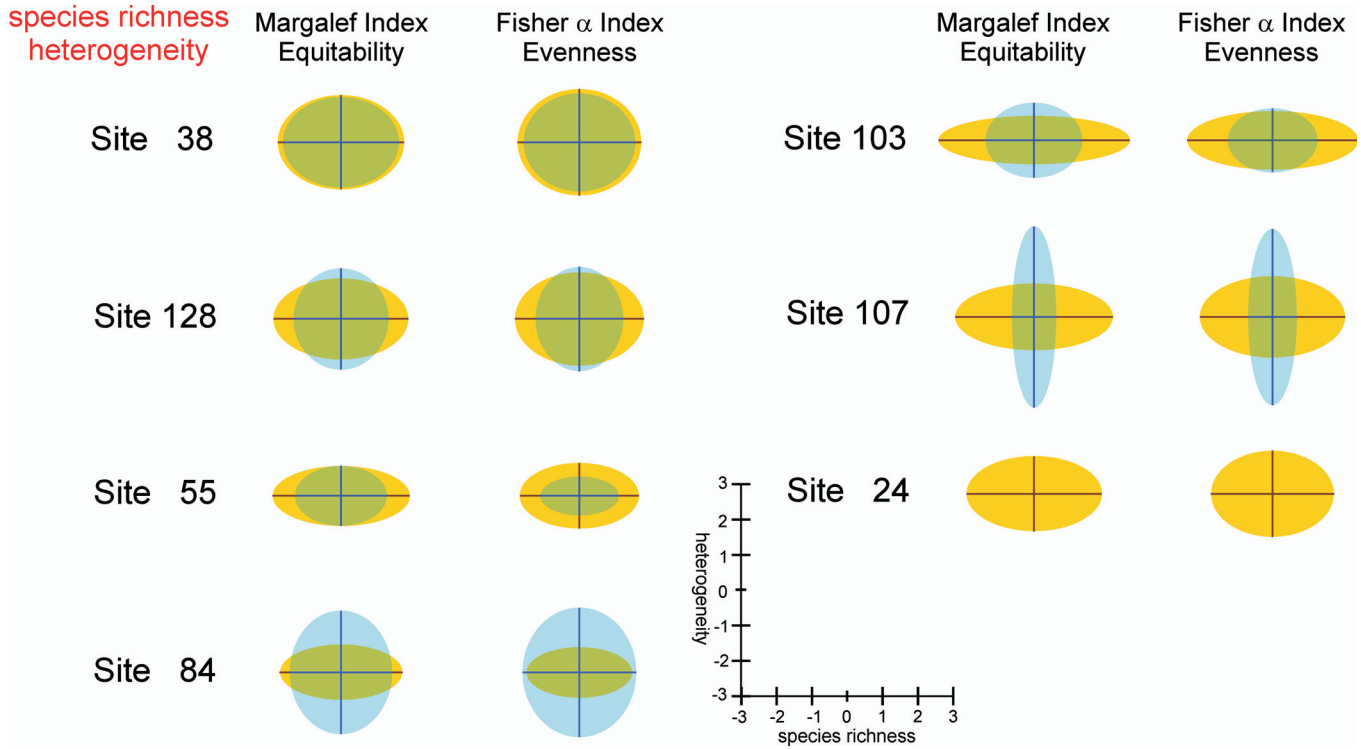
$$S_{Margalef} = (S_{observed} - 1) / \ln n \quad (\text{Eq. 3})$$

and the Fisher α -Index (Fisher et al. 1973)

$$S_{Fisher\alpha} = \alpha \ln(1 + n / \alpha) \quad (\text{Eq. 4})$$

Both scale-free indices cannot define the maximum number of species for the assemblage and are useful only for comparing samples, while S_{max} can be approximated with the index Chao 1 (Chao 1984)

$$S_{Chao1} = S_{observed} + f_1(f_1 - 1) / 2(f_2 + 1) \quad (\text{Eq. 5})$$



TEXT-FIGURE 4

Diversity diagrams of the selected sites from the Ria de Aveiro lagoon outlet (adapted from Martins et al. 2018) using different combinations of measures for species richness and heterogeneities.

where f_1 characterizes the number of species represented by a single specimen and f_2 the number of species with two specimens (Hammer 2016).

A further attempt to estimate species richness is by the individual rarefaction method (Sanders 1968) in its corrected version (Krebs 1999). Because the estimated number of species within a sample gained by the rarefaction method depends on the investigated specimen numbers n , the number of species S cannot be compared between samples with differing specimen numbers. Several methods have been developed making estimation of species richness by rarefaction possible, which is independent of sample size (e.g., Chao et al. 2014).

Heterogeneity. Contrary to species richness, heterogeneity indices incorporate densities of species characterizing the distribution form. For measuring heterogeneity, the most commonly used approaches in foraminiferal research are the ‘Simpson Diversity Index’ in biased form based on probabilities

$$D_{\text{Simpson}} = 1 - \sum_{j=1}^S \left\{ \left[\frac{n_j(n_j-1)}{n(n-1)} \right] \right\} \quad (\text{Eq. 6})$$

and the ‘Shannon Diversity Index’ H (Entropy) based on natural logarithms

$$H_{\text{Shannon}} = - \sum_{j=1}^S \left(\frac{n_j}{n} \right) \ln \left(\frac{n_j}{n} \right) \quad (\text{Eq. 7})$$

(Maurer and McGill 2011).

Normalizing heterogeneity measures to the limits 0 (complete dominance) and 1 (complete heterogeneity) is termed ‘Even-

ness’. Two measures are commonly used in foraminifera, both based on the Shannon Entropy. ‘Equitability’ (Hammer 2016) is defined by $H/\ln S$ (Pilou 1969) and ‘Evenness’ (Hammer 2016) by $e^{H/S}$ (Buzas and Gibson 1969). The Simpson Diversity Index can also be corrected by D_{Simpson} / D^* using the correction factor

$$D^* = 1 - \left[\left(\frac{n}{S} \right) - 1 \right] / (n-1) \quad (\text{Eq. 8})$$

COMPARISON AMONG LAs AND DAs

Using the four characteristics ‘total density’, ‘species density’, ‘species richness’ and ‘heterogeneity’, comparisons between LAs and DAs using combinations of these factors are possible. Weighting densities of LAs and DAs by similarities could raise the information content and relieves interpretation.

Incorporation Value

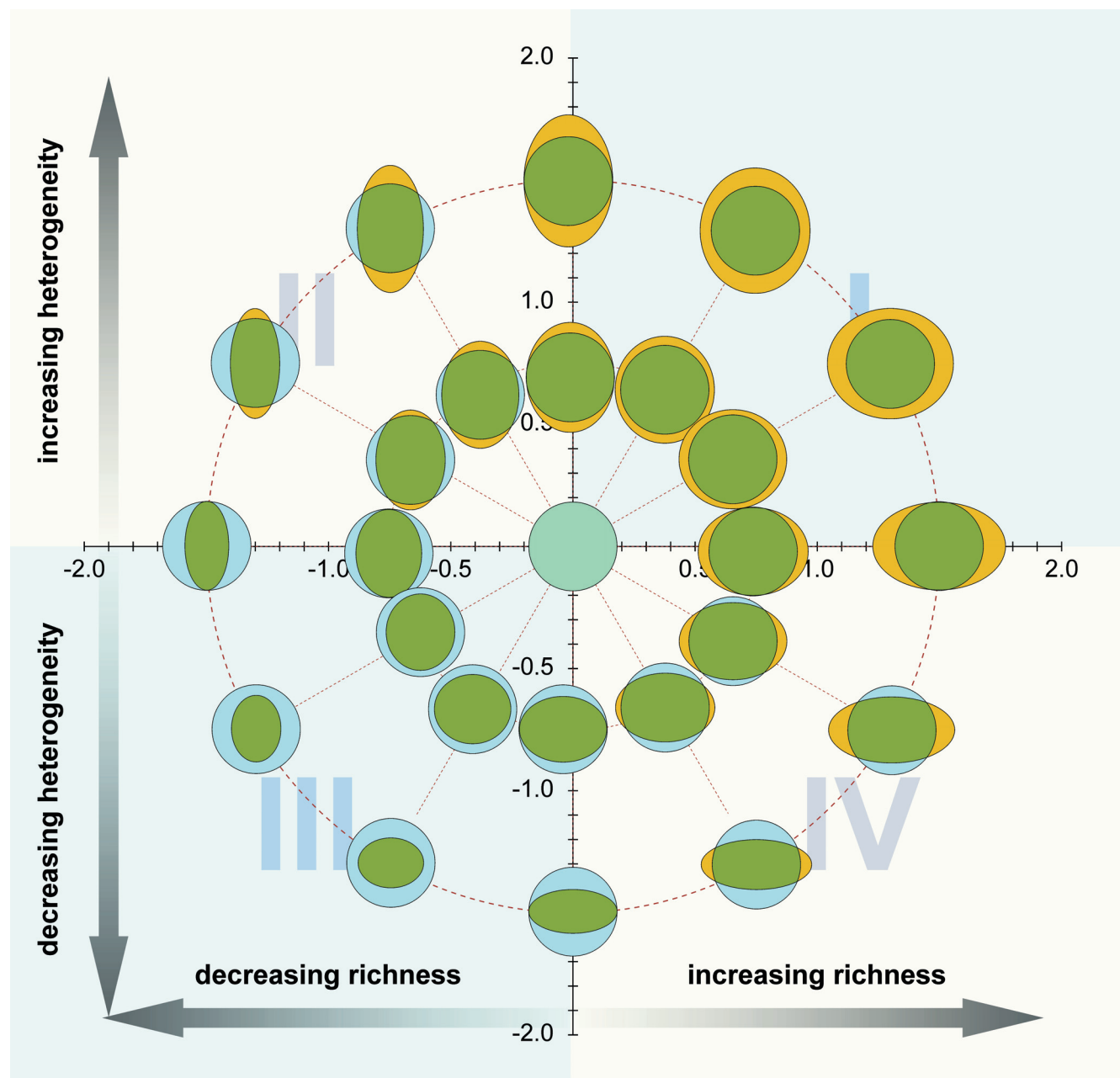
This index weighs the relation between densities of LAs and DAs by similarities between both assemblages. Thus it becomes independent from total density (LA plus DA). From a population dynamics point of view, this index demonstrates the integration grade of newcomers (instantaneous LA) into the time averaged DA.

The ‘Incorporation Value’ characterizing the k^{th} sample is introduced as

$$\text{IncorpVal}_k = \text{Receiving}_k \cdot \text{Similarity}_{k \text{ living dead}} \cdot 200 \quad (\text{Eq. 9})$$

with

$$\text{Receiving}_k = \text{density}_{k \text{ living}} / (\text{density}_{k \text{ dead}} + \text{density}_{k \text{ living}}) \quad (\text{Eq. 10})$$



TEXT-FIGURE 5

The effect of standardized vectors running from LAs to DAs. Standardized species richness and heterogeneity of the LAs determines the origin of the vector (e.g., species richness: 0, heterogeneity: 0); standardized vectors with length 0.75 and 1.5 rotating around the origin affects ellipses of the DA, but keeps the ellipse of the LAs constant (explanation in the text).

where every similarity index that varies between 0 (completely dissimilar) and 1 (completely similar or identity) can be used. Particularly, the Bray-Curtis Similarity Index (Bray and Curtis 1957), the Cosine (Orloci 1966), the Renkonen Index (Renkonen 1938) and the Jaccard Index based on abundances (Chao et al. 2005) can be used.

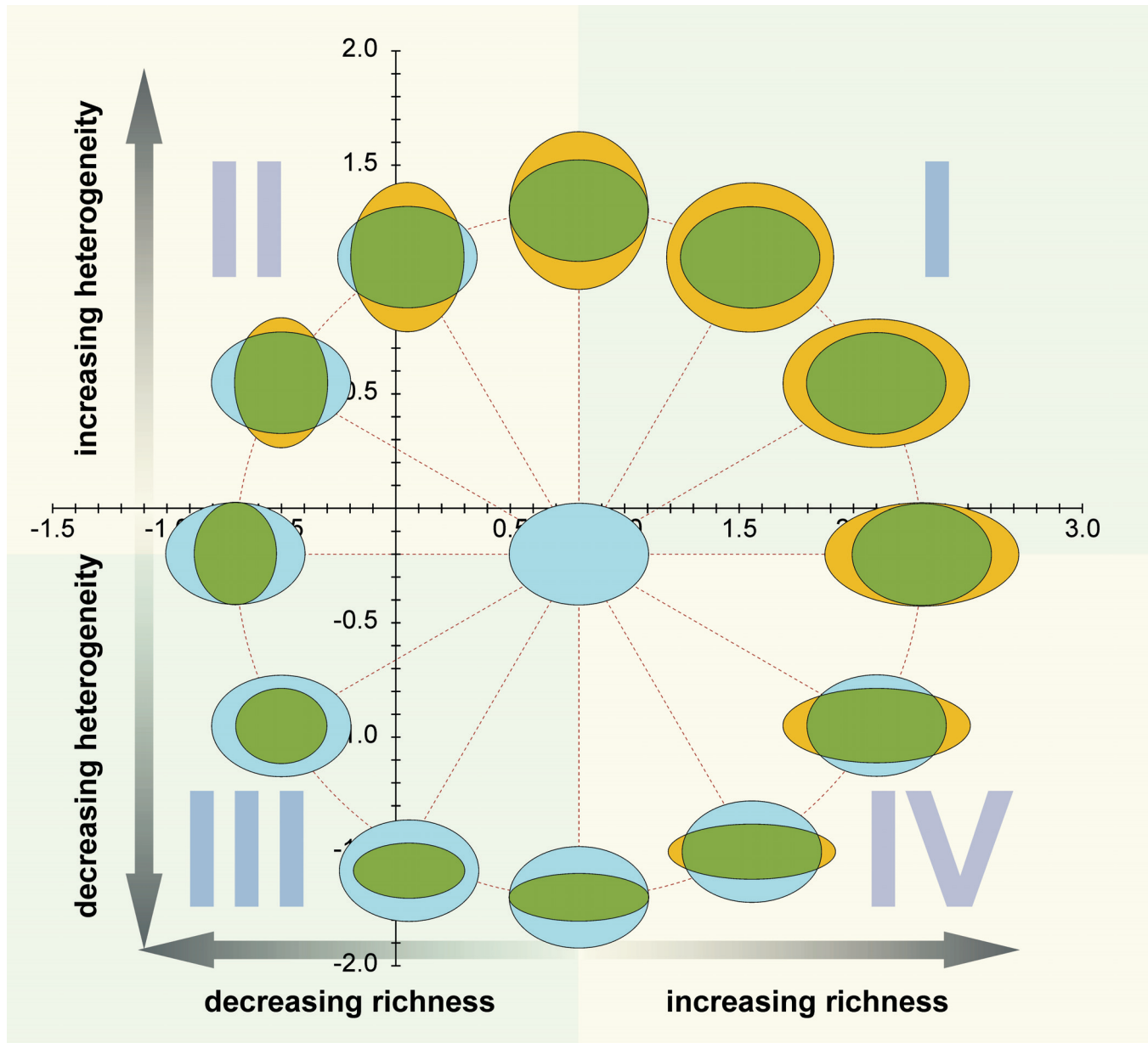
While ‘Receiving’ characterizes the proportion of LAs on total assemblages varying between 0 (total lack of LA) and 0.5 (slightly higher total density of LA than DA), ‘Similarity’

marks the concordance in species composition between LA and DA.

The same magnitudes of ‘Incorporation Values’ can either be caused by high ‘Receiving’ combined with low ‘Similarity’ or vice versa. These hyperbolic relations are demonstrated in text-fig. 2 by isolines marking identical ‘Incorporation Values’.

Standardized diversities

Species richness and heterogeneity can simultaneously be compared between LAs and DAs. In this case, diversity measures



TEXT-FIGURE 6

The effect of standardized vectors running from LAs to DAs. Based on different origins in LA (e.g., species richness: 0.8, heterogeneity: -0.2); the standardized vector with length 1.5 rotating around the origin affects ellipses of the DA, but keeps the ellipse of the LAs constant (explanation in the text).

must be transferred to comparable numerical scales possessing identical ranges. Therefore, any index for species richness or heterogeneity can be used. Comparable scales can be obtained by standardization

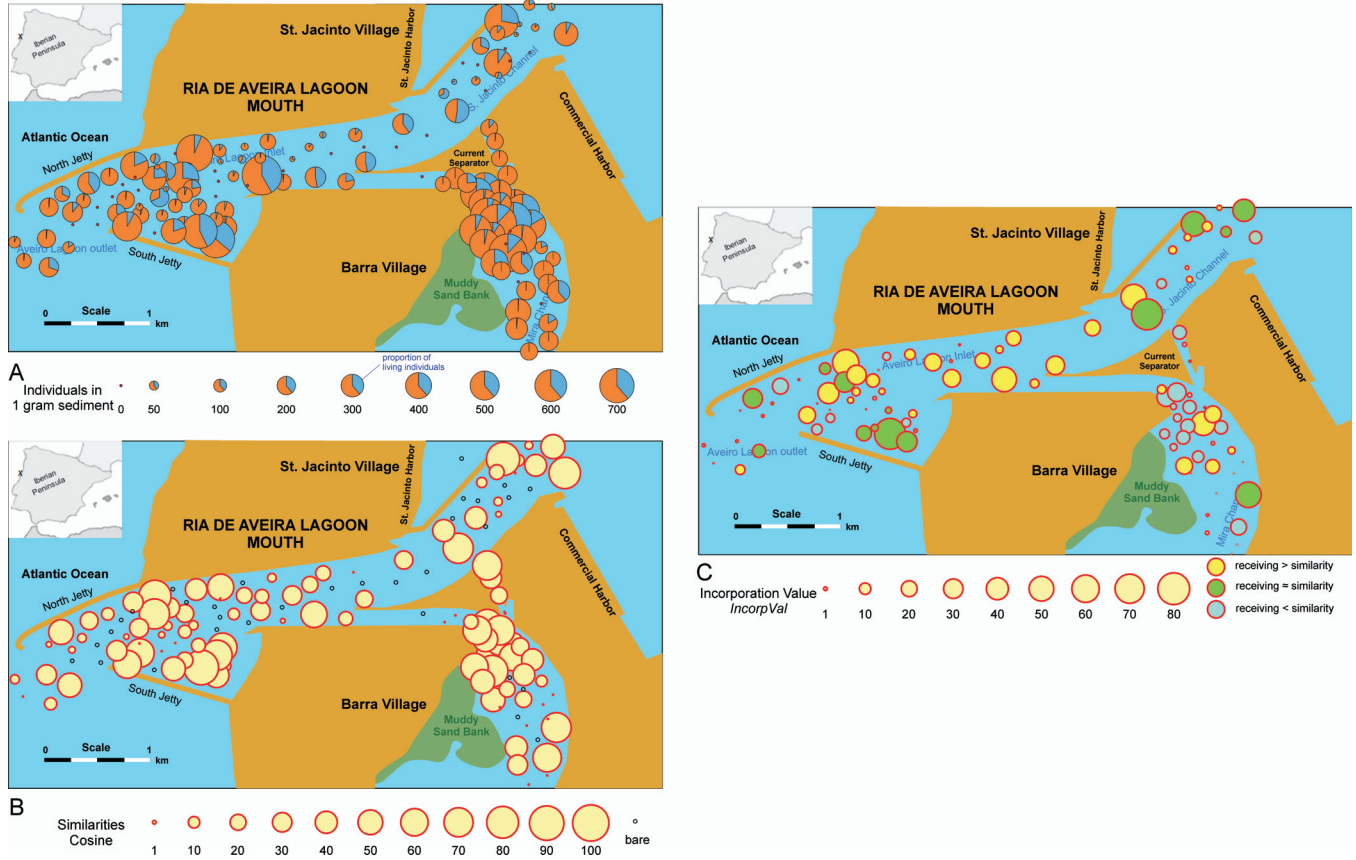
$$x_{k \text{ living}}^* = (x_{k \text{ living}} - \bar{x}) / \sigma \quad (\text{Eq. 11a})$$

$$x_{k \text{ dead}}^* = (x_{k \text{ dead}} - \bar{x}) / \sigma \quad (\text{Eq. 11b})$$

where the mean and standard deviation must be calculated over all LAs as well as DAs used in the study. Species richness and heterogeneity separately act as x -values in the equations above.

Note that standardization relates to the number of investigated sample sets in a distinct region. Accordingly, the original total mean and standard deviation must be given in the investigation (text-fig. 3B) to enable recalculation of the original values of species richness and heterogeneity. This dependence on sample numbers within a region makes comparisons between regions impossible when their parameters have been separately standardized. To compare several regions, the parameters must be simultaneously standardized over all regions under investigation.

Diversity diagrams. Diversities of LAs and DAs can be represented in a coordinate system, where species richness is posi-



TEXT-FIGURE 7

Comparison between density measures and the Incorporation Values in the Ria de Aveiro lagoon mouth (Martins et al. 2018). (A) Distribution of densities, (B) Distribution of 'Similarities, (C) Distribution of 'Incorporation Values'.

tioned on the x-axis and heterogeneity on the y-axis. Comparable scales in both axes are obtained by standardization (text-fig. 3A). To include samples lacking LAs, all standardized values are transformed to

$$x_k^* \text{ transformed} = x_k^* + 3 \quad (\text{Eq. 12})$$

Before transformation, samples lacking LAs receive the values -3 for species richness and 3 for heterogeneity. The limits of three standard deviations are chosen because 99.9% of observations are positioned within the range -3σ and $+3\sigma$, setting the range of standardized values from 0 to 6.

Diversity diagrams are independent of the type of diversity measures; each measure of species richness can be compared with each measure of heterogeneity. Different combinations are shown in text-fig. 4 using the selected samples from the Ria de Aveiro outlet (Martins et al. 2018) showing similar diversity diagrams.

Standardized Vectors. The vector between both standardized species richness and heterogeneity in the above-mentioned coordinate system demonstrates relations between LA and DA. It is determined for sample k by

$$\text{Length}_{k \text{ living dead}} = \sqrt{(SR_{k \text{ living}}^* - SR_{k \text{ dead}}^*)^2 + (H_{k \text{ living}}^* - H_{k \text{ dead}}^*)^2} \quad (\text{Eq. 13})$$

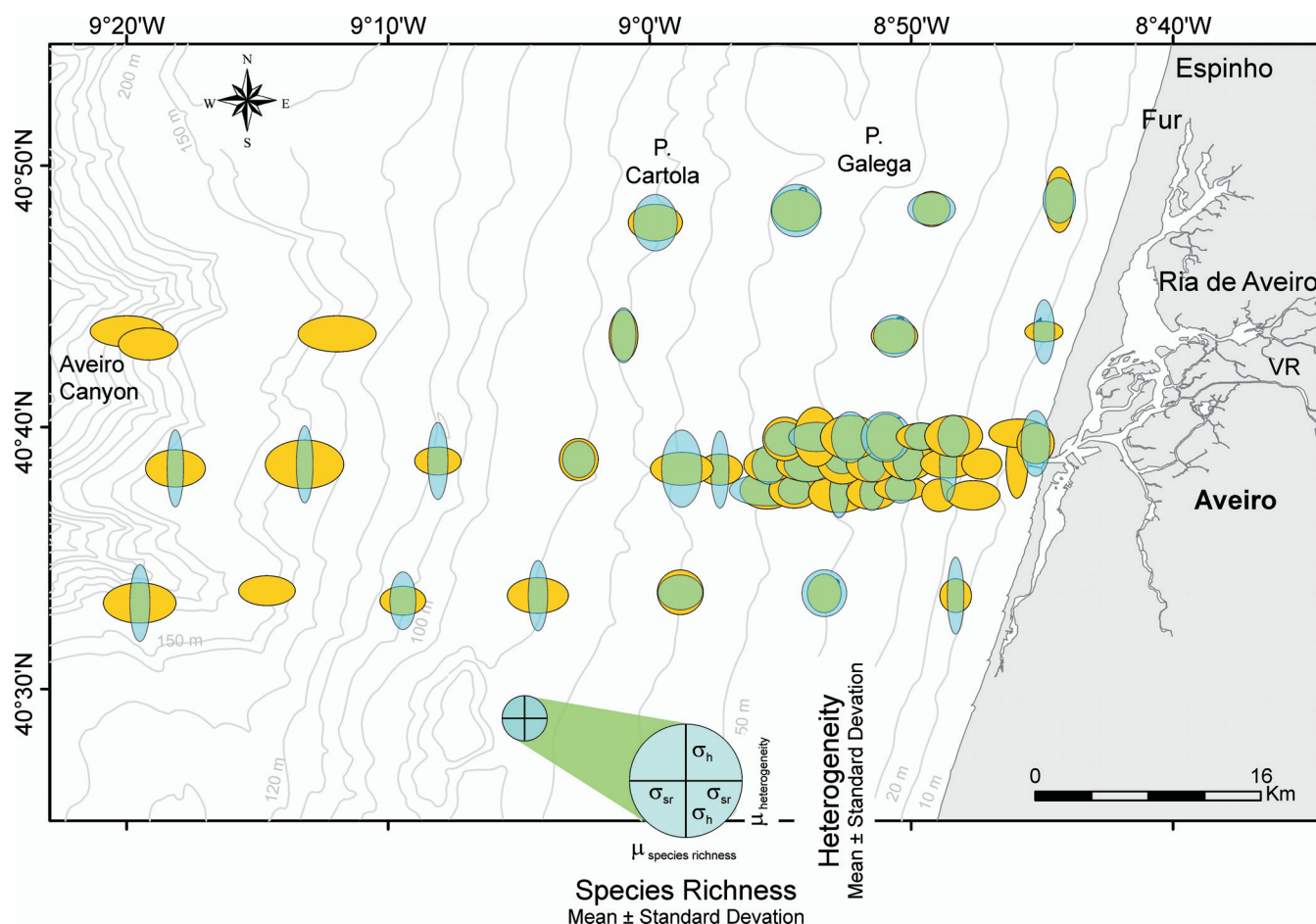
and

$$\text{Angle}_{k \text{ living dead}} = \arctan \left[(H_{k \text{ living}}^* - H_{k \text{ dead}}^*) / (SR_{k \text{ living}}^* - SR_{k \text{ dead}}^*) \right] \quad (\text{Eq. 14})$$

in radians (text-fig. 3B)

'Length' determines the difference in diversities between LAs and DAs, i.e., large \rightarrow weak accordance, short \rightarrow high accordance. The orientation of the vector (Angle) shows the relation in diversities divided into quadrants, where the standardized values for species richness and heterogeneity of LA_k determine the origin of the coordinate system (text-figs. 5, 6).

Based on this coordinate system, angles between 0° and 90° (quadrant I) as well as between 270° and 360° (quadrant IV) point to increasing species richness in DAs compared to LAs (maximum at 0°), while angles from 90° to 270° (quadrant II and III) show the opposite trend of decreasing species richness compared to LAs (minimum at 180°). In quadrants I and II (0° to 180°), heterogeneity in DAs are higher than in LAs, peaking



TEXT-FIGURE 8

Distribution of 'Diversity Diagrams' in offshore transects off the Ria de Aveiro lagoon (Martins et al. submitted).

at 90°, while from 180° to 360° (quadrants III and IV) the heterogeneities of DAs are lower than those of LAs, with a minimum at 270° (text-figs 5, 6).

IMPROVEMENT OF INDICES

Here, we checked the singularities of the new indices and their advantages against the normally used measures of densities, diversities and similarities for comparing LAs and DAs based on 105 samples from the Ria de Aveiro lagoon outlet (Martins et al. 2018) and on 44 samples from the shelf off the Ria de Aveiro lagoon (Martins et al. submitted). The coefficient of variation ($CV = \sigma/\mu$) is used as a measure of information content (Zar 2010), where its magnitude characterizes the information gain.

First, densities and similarities of LA and DA are compared with Incorporation Values for the Ria de Aveiro lagoon outlet (Martins et al. 2018). Densities are higher at the borders of the S. Jacinto Channel and the Aveiro lagoon outlet and low to lacking in the center of both channels (text-fig. 7A). They are much higher in protected regions north of the southern jetty and within the Mira Channel. Similarities between LAs and DAs show different distributions although they are high in protected regions and at the border of the main channel (text-fig. 7B). The Incorporation Values allow a deeper insight into the integration

of living individuals to the total assemblages (text-fig. 7C). The low Incorporation Values in the S. Jacinto Channel and the Aveiro Lagoon outlet are remarkable. Furthermore, relations between 'Receiving' and 'Similarity' differ between the main channel regions including the protected area near the south jetty, where 'Receiving' dominates 'Similarities' (yellow points in text-fig. 7C), and the Mira Channel samples, where opposite relations dominate (blue points in text-fig. 7C). The information content is much higher for the Incorporation Value ($CV = 1.24$) compared to total densities ($CV = 0.32$), densities of living individuals ($CV = 1.11$), densities of dead individuals ($CV = 0.48$) and the proportion of living individuals to total densities ($CV = 1.11$).

These results based on descriptive statistical methods allow the following interpretations: The center of the main channels dug by man to prevent sediment accumulation shows the lowest or lacking total densities with either low occurrences or devoid in living foraminifera. Protected areas along the border of channels or in areas sheltered by jetties enable normal sediment accumulation and the settlement of living specimens, resulting in high total densities and high proportions of living individuals, sometimes higher than densities of dead specimens (text-fig. 7A).

The distribution of Incorporation Values (text-fig. 7C) in the investigation area allows to discriminate different patterns in the lagoon mouth area. Dominance of similarities (blue circles) is observed in protected areas of the Mira Channel entrance where the bottom is stable and there is a good connection with the ocean allowing the development of living assemblages and the record in dead one of previous generations of foraminifera. The main influence by proportions of living/total densities (yellow circles; text-fig. 7C) is observed mostly in the São Jacinto Channel and in the lagoon inlet denoting the recent recolonization and repopulation of sites after disturbing events, which caused the removal of empty tests of foraminifera. Only in a few sites this effect is observed in the Mira Channel.

The highest balance between receiving and accordance (green circles in text-fig. 7C) is mostly found near the walls that delimit the channels and the inlet (in protected areas) where the bottom sediment was stable during a relatively long period and under strong marine influence.

Diversity diagrams based on standardized diversity measures are shown for shelf transect samples offshore the Ria de Aveiro mouth (Martins et al. submitted) ranging from 5 to 190 m depth (text-fig. 8). While in shallow samples down to 20 m specimens are rare both in LAs and DAs, they become abundant between 30 and 50 m with high proportions of living individuals, exemplified by species number as well as heterogeneities. These parameters are similar for the dead individuals leading to characteristic diagrams. With increasing depth, living individuals become rare to absent expressed in diagrams showing only dead individuals, characterized by high species richness but low heterogeneities (text-fig. 8).

Nonmetric multidimensional scaling based on the standardized diversity measures for LAs and DAs including the environmental factors depth, TOM and grain-size together with the standardized Vector Lengths and Vector Angles shows the relations between the diversity diagrams and these factors (text-fig. 9). The strongly correlated environmental factors water depth and percentages of TOM are mainly represented along scale 1. Here, the trend in LAs and DAs from almost coincident diversities in LAs and DAs at high coordinate values to high species richness/low heterogeneities in DAs and low to missing species richness coupled with high heterogeneities in LAs at low coordinate is characteristic.

Following the grain size vector that is almost independent from depth and TOM, the increase of species richness with more or less constant heterogeneities is characteristic for DAs. Along this gradient, LAs start with species numbers of 0 at low gradient values becoming almost identical with the high species numbers of DAs at highest gradient values. On the contrary, heterogeneities of LAs are high at low values of the grain size vector and approximate heterogeneities of DAs at high grain size values (text-fig. 9).

These descriptive data lead to the following interpretation: Sedimentary dynamics influence the distribution of foraminifera in this region. Densities of DAs increase, in general, towards the deeper continental shelf zones correlated with an increase in fine-grained sediment and TOM due to reduced removal of foraminiferal tests by hydrodynamic activity and low dilution of tests by terrigenous inputs at these depths. Densities of LAs are higher between 30 and 50 m at gravelly deposits of the mid shelf. The stability of the substrate coupled with good oxygena-

tion and high availability of organic matter from marine productivity, supplied by the lagoon of Aveira, allows the development of large LAs at this depth zone. The accumulation of empty tests in deep areas or remobilization, transport and dispersion of tests by hydrodynamic forces at shallower stations leads to the lack of LAs in both regions.

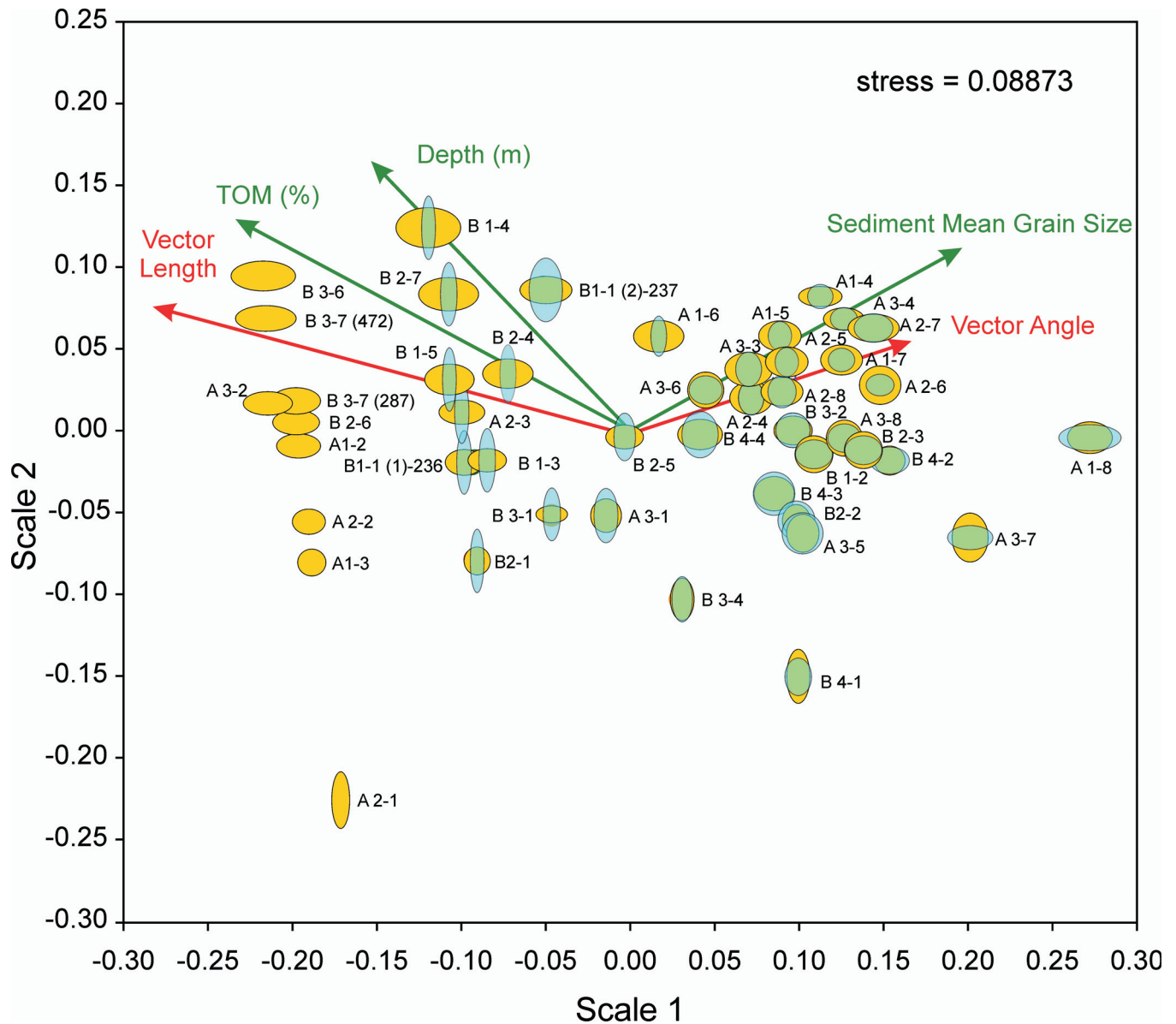
REASONS FOR DIFFERENCES AMONG LAs AND DAs IN FORAMINIFERA

Many papers are written to explain the differences between LAs and DAs especially for mollusks that are less abundant per unit squares and almost much longer living than foraminifera (e.g., Kidwell 2013; Kidwell and Tomašových 2013). When interpreting relations between LAs and DAs in foraminifera, it must be noted that LAs reflect the instantaneous environmental situation at sampling time, which can change during longer time intervals (e.g., seasons) due to different factors. Furthermore, the extreme patchiness of benthic foraminifera in the intertidal and shallow subtidal hinders the exact estimation of LAs at the surrounding of a sampling station, while DAs, in contrast, remain more constant representing time-averaged assemblages (Armynot du Chatelet et al. 2017) that can be altered by fossilization processes (Martin 1999).

In addition, significant differences between instantaneous living assemblages and time-averaged death assemblages can be caused by various biotic and abiotic factors. For foraminifera, seasonal and annual changes of factors such as temperature, salinity or pH influence the reproduction onset and life-time (e.g., Murray 1976, Avnaim-Katav et al. 2016). Additionally, population dynamics with differences in offspring numbers and survival rates lead to strong variations in the abundance decrease during life-time (e.g., Murray 1976, Hohenegger et al. 2014). Variable bottom and surface current intensities and directions due to seasons, including spring tides, wind-induced currents and particularly the influence of storms, lead to a selective or complete loss of species by transport. The crossing of the south-westerly storms (rainy season), typical of the winter oceanographic regime, also strengthens currents in the investigated area, namely in shallow-water environments, lowers pH in the intertidal and leads to eu- and hypertrophication by importing organic material. In combination with short- and long-term pollution, species react with different sensibilities and intensities, again leading to selective or complete loss. Moreover, the selective resettlement by species after loss or displacement may promote difference in composition and abundance between LAs and DAs. In benthic foraminifera, resettlement by propagules that can rest for months or years under unfavorable conditions in fine-grained sediments, starting growth when conditions become favorable, is important in shallow marine environments (Alve and Goldstein 2002, 2003). Beside these propagules, other types of dormancy during life-time allows survival under unfavorable conditions (Ross and Hallock 2016).

CONCLUSIONS

Primarily, sample densities and species densities should be used when comparing assemblages. In contrast, proportions (percentages), although linearized for using parametric statistics, and stopped counting at some defined number lead to interdependence of species frequencies. Based on these distortions, the latter approach cannot represent the latent densities in species distributions investigating the response of species abundance to a gradient.



TEXT-FIGURE 9

Diversity diagrams of sample sites of Text-fig. 8 positioned in a coordinate system obtained by nMDS based on standardized species richness and heterogeneities for LAs and DAs. Influence of environmental factors water depth, mean grain size and TOM represented as vectors together with the variables standardized diversity vector's length and angle (Martins et al. submitted).

The LA and DA of a sample (site, etc.) can be compared by total densities, species densities, similarities and by the diversity measures 'Species Richness' and 'Heterogeneity'. Weighting of these measurements gives deeper insights into the relations between both assemblages allowing a better knowledge and characterization of the environmental prevailing conditions in the study area.

The 'Incorporation Value' as a measure of concordance weighs the proportion of LAs on total densities (Receiving) with similarities in species composition between LAs and DAs. This approach shows the grade of integration at the time in point when the sample was taken. The 'Incorporation Value' obtained from

one sample characterizes an instantaneous situation. Taking several samples from an identical site over a longer time interval (1 year) enables calculating 'Time Averaged Incorporation Values' simultaneously acting as replicates for DAs. In this study only the results of a single sampling event are analyzed, but the comparison between LAs and DAs highlights the effect of different hydrodynamic conditions and allows to distinguish recently disturbed and recolonized (recovered) sites from others, where the degree of disturbance caused by instabilities of bottom sediments has been continued for a relatively long period.

Working with standardized diversity measures enables a simultaneous comparison of species richness and heterogeneity be-

tween LAs and DAs. ‘Diversity Diagrams’, in which species richness is presented on the abscissa and heterogeneity on the ordinate, visually demonstrate the differences between LAs and DAs. Starting from the coordinates of LAs, differences in both diversity measures to the DA can be represented by ‘Standardized Vectors’, with the vector’s length determining the magnitude of differences. The vector angle shows the orientation of the vector towards increasing/decreasing species richness along the abscissa, with maximum at 0° and minimum at 180° retaining the same heterogeneities in LA and DA. Increasing/decreasing heterogeneity oriented at the ordinate has its maximum at 90° and minimum at 270° with identical species richness in both assemblages.

The comparison of LAs and DAs using ‘Diversity Diagrams’ allows to verify the similarity in terms of composition of both assemblages in the study area.

Note that all indices using standardized diversity measures failed in comparing different regions because of their variable sample numbers. They can, however, be used after recalculating standardization based on the sample set combined over the considered regions.

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