APPENDIX DR1: METHODOLOGICAL DETAILS AND INFORMATION

METHODS

Fossil datasets (Appendix DR2) were downloaded from the Paleobiology Database (PBDB: https://paleobiodb.org) on 03/18/2018 using the following query: http://paleobiodb.org/data1.2/occs/list.csv?datainfo&rowcount&taxon_reso=species&pres=regular&envtype=!terr,unknown,lacust,fluvial,karst,terrother&all_records&show=full,attr,class,classext,genus,subgenus,acconly,ident,img,plant,abund,ecospace,taphonomy,etbasis,pres,coords,loc,paleoloc,prot,strat,stratext,lith,lithext,env,geo,methods,rem,resgroup,ref,refattr,ent,entname,crmod,acconly. The PBDB datasets that are sufficiently densely sampled for our analyses are clustered in North America and Europe (Figure DR1A) (Alroy et al., 2001) and primarily deposited in deep to shallow subtidal shelf settings.

Modern datasets were downloaded via the Ocean Biogeographic Information System (OBIS: http://www.iobis.org) and its various regional partner sites. We downloaded all datasets that included quantitative abundances of all benthic macrofauna and megafauna from multiple benthic grab or trawl samples in a region. The only datasets with sufficiently dense sampling included in our analyses were:
Benthos of the Danish shelf (ODAM): http://www.iobis.org/explore/#/dataset/3920
Benthos of the Swedish shelf (SHARK): http://www.iobis.org/explore/#/dataset/3826
Benthos of the North Sea: http://iobis.org/explore/#/dataset/586
Benthos of the Cretan shelf: http://www.iobis.org/explore/#/dataset/3185
Benthos of the Adriatic shelf: http://www.iobis.org/explore/#/dataset/2645
Benthos of the eastern English Channel: http://iobis.org/explore/#/dataset/710
Benthos of the Scheldt Estuary, Belgium: http://iobis.org/explore/#/dataset/2977
The EPA EMAPS dataset (USA) http://www.iobis.org/explore/#/dataset/25

For the rest of the discussion here, we will refer to the former seven datasets collectively as the EurOBIS database (Appendix DR3, Figure DR1B: orange points) and the latter as the EMAPS database (Appendix DR4, Figure DR1B: blue points). We used associated substrate data to constrain habitat in the EMAPS database. Substrate data are inconsistently reported in the EurOBIS database, so to constrain habitat for European samples we intersected sample coordinates with shapefiles from the EMODnet broad-scale benthic habitat maps (http://www.emodnet-seabedhabitats.eu/default.aspx) using QGIS (https://www.qgis.org/en/site/).
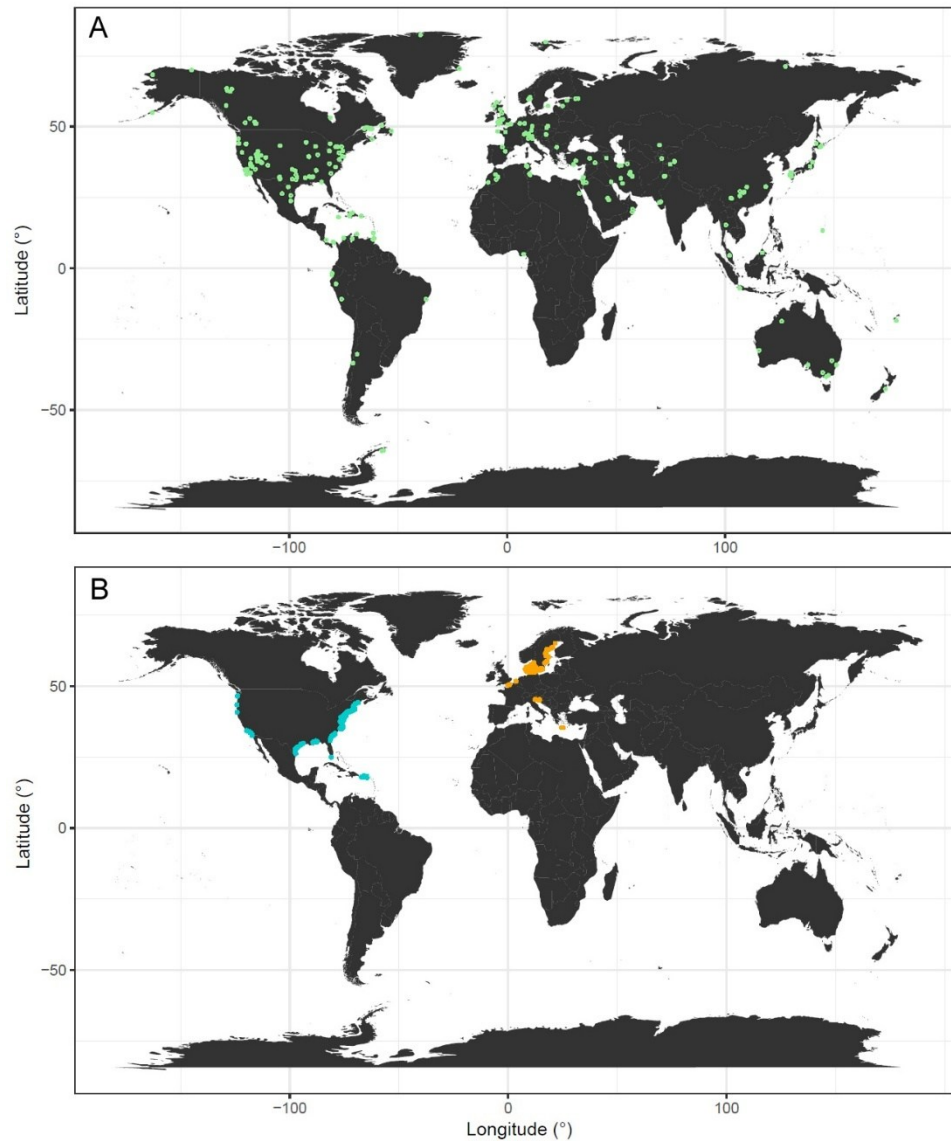
Figure DR1. Geographic origin of the data used in this study using the maximum database sizes used in this study. A: Paleobiology Database (n = 301). B: EMAPS database (n = 170, left, blue) and EurOBIS database (n = 137, right, orange).

The accuracy of the latitudinal and longitudinal coordinates of localities varied in the PBDB data and only those records accurate to minutes (two decimals) and seconds (three to four decimals) were selected for further analyses. The PBDB data contains information on locality, age, life habit, environment, stratigraphic formation and member, and sedimentology. Besides taxon and precise locality information, the assembled EurOBIS database also contains information on substrate, depth (mostly < 50 m), energy levels, and collecting date for most taxon occurrences, while all except energy levels are also recorded for the EMAPS database. The EMAPS database consistently has latitudinal and longitudinal coordinates accurate to three decimals, whereas EurOBIS database coordinates mostly consist of at least two decimals. For the modern databases, not all Linnaean taxonomic levels were available so the WoRMS database was used to assign families, orders, classes, and phyla to respective genera. All taxa not

determined to the species-level were removed and only benthic organisms were selected for further analyses for all databases.

For species co-occurrence analyses on presence/absence datasets, we used the R-package cooccur 1.3 (Griffith et al., 2016), which is a probabilistic model of species co-occurrence (Veech, 2013, 2014) to a set of species distributed among sampling sites or localities with a given area. This model computes the observed and expected frequencies of co-occurrence between all species pairs for a species pool. For each species pair, two probabilities are calculated: the probabilities that the observed co-occurrence value is lower and higher than expected by chance. The alfa for species pairs to be classified as either aggregated or segregated is 0.05. The model returns significance levels for both aggregated or segregated species pairs. Only species pairs that have an expected co-occurrence of > 1 are used to remove species pairs from the analysis that do not have sufficient occurrence data (see Veech, 2013; Griffith et al., 2016). Co-occurrence probabilities are calculated using the combinatorics (Veech, 2013) and the faster hypergeometric distribution approach (Griffith et al., 2016); both yielding identical probabilities. We did not use abundance data to analyze co-occurrence patterns (Ulrich and Gotelli, 2010) herein because such data is inconsistently present.

Species pools ('datasets' here) were defined as follows: (a) The geographic area in which species could have interacted is defined as a 0.2° longitude x 0.2° latitude area (= 22.2 km x 17.1 km at 40° latitude; most data originate from 30–60°N) to maximize sample size per taxonomic category. This definition is somewhat arbitrary but is intended to minimize turnover along geographic, bathymetric, and substrate gradients (see also sensitivity tests discussed below). (b) At least ten species and ten localities or sites within the predefined area to ensure a substantial number of species pairs per species pool (Lavender et al., 2016; Veech, 2013).

To test whether congeneric species formed segregated species pairs more often than more distantly related pairs, as predicted by the competitive-relatedness hypothesis (Darwin, 1859; Cahill et al., 2008), six levels of taxonomic distance were used to identify truly random, aggregated, and segregated species pairs: (1) congenerics; (2) species in the same family but different genera; (3) species in the same order but different families; (4) species in the same class but different orders; (5) species in the same phylum but different classes; and (6) species pairs from different phyla. A similar approach, using phylogenetic distance instead, was employed for experiments with bacteria (Violle et al., 2011). Estimating phylogenetic distance for all species pairs in our analyses (modern and fossil databases) was not feasible because of the vast number of species from various phyla. Boxplots are used to show the percentage of segregated pairs of all possible pairs per dataset per taxonomic distance category. Only datasets with at least ten species pairs (= truly random + aggregated + segregated pairs) are used to minimize the effect of small sample sizes on the percentage of negative pairs of all possible pairs per dataset, yet ensure an as high as possible number of total datasets per taxonomic category. To avoid incorporating incorrect segregated congeneric species pairs, such pairs were checked for possible synonymies, spelling errors, and whether one of the two species is currently placed in a differing genus using the WoRMS database for extant species and the primary literature for fossil species. Competitive exclusion can be detected using the methods herein: see Figure DR2 for an example of a dataset of modern finches that are known to compete heavily for resources (Sanderson, 2000).

For the PBDB data, a very restrictive method was used, where environment, stratigraphic formation and member, biostratigraphic zone, minimum and maximum age, detailed lithology (facies), and stratigraphic scale (bed, member, formation) were the same for each dataset. To test whether any differences existed among eras, the Paleozoic, Mesozoic, and Cenozoic eras were analyzed separately. To test the sensitivity of the results, the geographic area in which species could have interacted was changed into much smaller areas as allowed by sample size (0.1° x 0.1°, 0.05° x 0.05°, and 0.01° x 0.01°). Furthermore, we also tested whether the degree of taxonomic identification to the species-level had any influence on the results by analyzing only datasets with ≥ 50% and ≥ 75% of all taxa determined to the species-level. We also used the finest stratigraphic scale of beds to minimize possible temporal turnover for all datasets and also separately for Cambrian Konservat-Lagerstätten, deposits that are minimally affected by time-averaging and preserve soft-bodied animals so that they are as close to ecological snapshots as possible for the fossil record. Finally, we calculated the percentages of all aggregated pairs of all species pairs across taxonomic categories for comparison to modern data.

A variety of subsets and groupings of the EurOBIS database were analyzed to test the sensitivity of the analyses: (a) all taxa; (b) taxa from 0–20 m water depth to minimize the potential detection of segregated pairs due to depth gradients; (c) taxa collected from 1995–2014 to minimize the potential detection of segregated pairs due to species short-term turnover; (d) taxa grouped by substrate to analyze species pairs that occur in the same type of substrate only; (e) taxa grouped by energy level to analyze species pairs that occur in the same type of energetic environment only; (f) taxa from 0–20 m depth grouped by substrate and energy level as a very strict way to ensure similar environmental conditions. The EMAPS database is too small for these groupings and subsets except for (a). Some samples, particularly those from English Channel and the Scheldt Estuary, appear to have been collected by dredging and trawling, which may bring together species that are separated in nature and thus potentially erase segregated species pairs. Such data are excluded to assess grab samples only.

The EurOBIS database was also used to evaluate the frequency of segregated species pairs at various depths (0–10, 10–20, 20–40, and 40–60 m) for areas of 0.2° x 0.2° and 0.1° x 0.1°. Greater depths and smaller areas yielded insufficient datasets per taxonomic distance. Additionally, smaller depth intervals within the deepest interval were also analyzed (i.e., 40–50, 50–60, and 45–55 m). The English Channel was also analyzed separately because 6/9 datasets from waters deeper than 40 m within our criteria originate from there. The EMAPS database was too small for the similar analyses. Likewise, selecting deeper water datasets from (qualitative) "offshore" environments for the PBDB data yielded insufficient data for congenerics.

Because the taxonomic composition differs between fossil and modern databases (Table DR1), mostly due to a lower preservation potential of poorly to non-calcified animals, occurrences of Mollusca, common in all databases and shown to exhibit good live-dead agreement in species composition (Kidwell and Flessa, 1995) and in species rank abundance (Kidwell, 2001, 2002), were selected for comparative analyses. The EurOBIS and PBDB data were used for this purpose and datasets with at least five species pairs were used to increase sample size per taxonomic category. All analyses were performed in R 3.3.1.
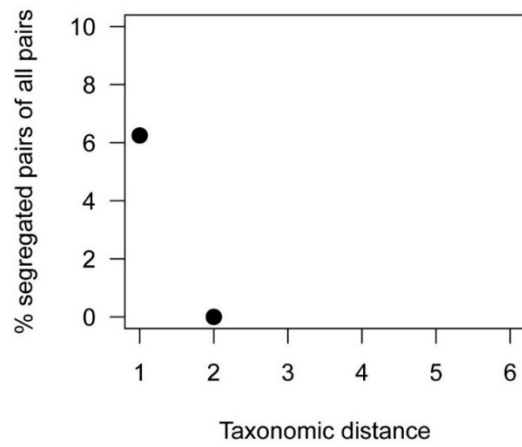
ADDITIONAL FIGURES

Figure DR2. Confamilial finches (family Thraupidae) from Galápagos that are suggested to have competed for resources leading to competitive exclusion (Sanderson, 2000). Number of species pairs: 16 and 47 for taxonomic distances 1 and 2, respectively.
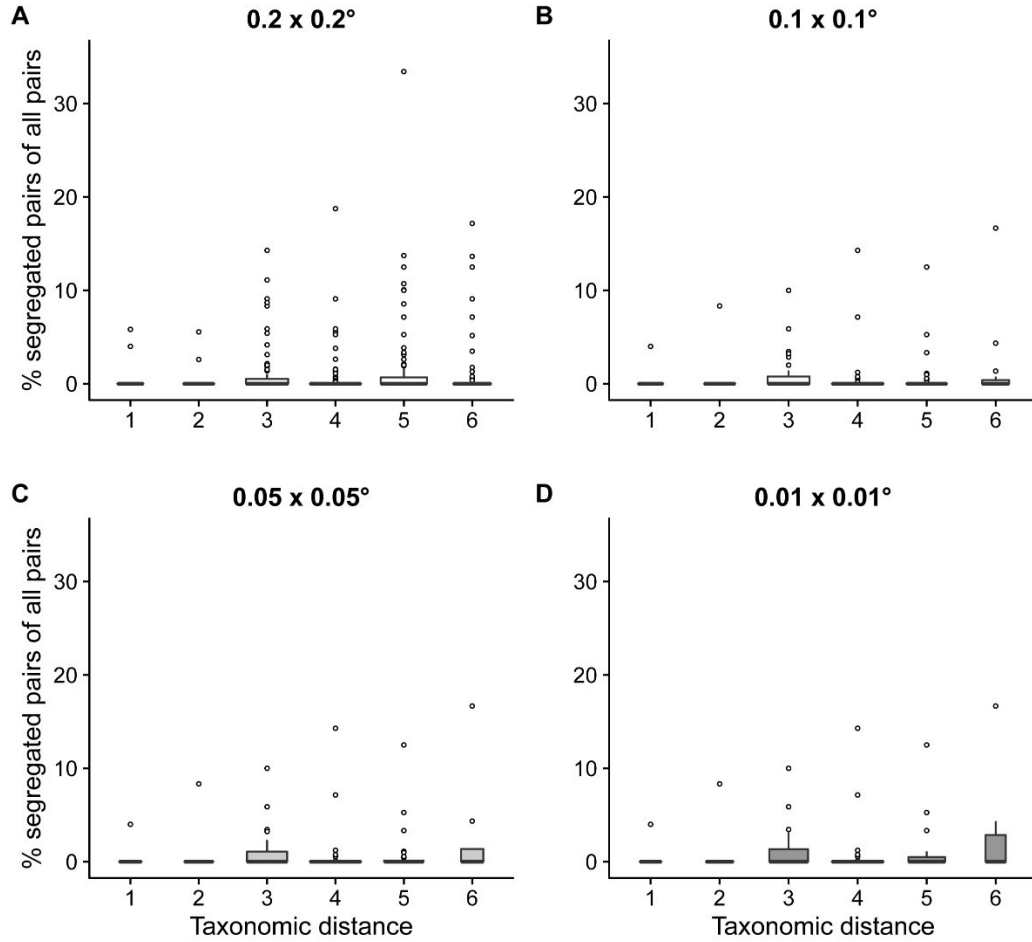
Figure DR3. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the Paleobiology Database. Minimum number of species pairs per data point is 10. Boxplot width is proportional to amount of data within each plot. A: Geographic area per species pool = 0.2° x 0.2° (=Figure 1A), sample sizes per taxonomic distance: 27–104. B: Geographic area per species pool = 0.1° x 0.1°, sample sizes: 13–55. C: Geographic area per species pool = 0.05° x 0.05°, sample sizes: 9–47. D: Geographic area per species pool = 0.01° x 0.01°, sample sizes: 7–46.
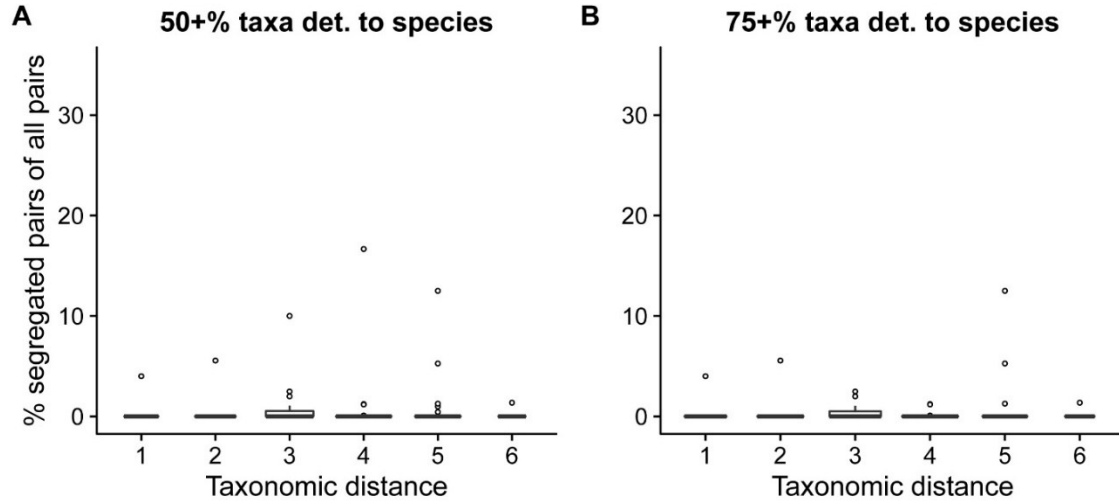
Figure DR4. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the PBDB data. The minimum number of species pairs per data point is 10. Geographic area per species pool = 0.2° x 0.2°. Boxplot width is proportional to sample size within each plot. A: At least 50% of all taxa within each dataset is determined to the species-level, sample sizes per taxonomic distance: 9–37. B: At least 75% of all taxa within each dataset is determined to the species-level, sample sizes: 7–25.
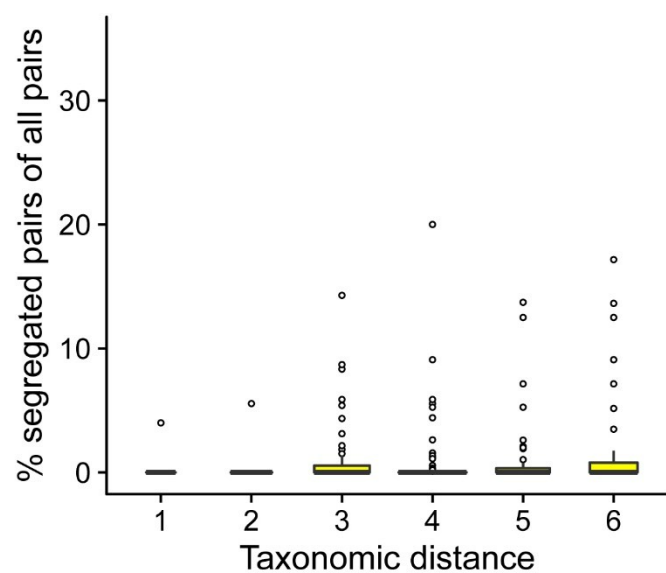
Figure DR5. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the PBDB data using the stratigraphic scale of beds only. The minimum number of species pairs per data point is 10. Boxplot width is proportional to sample size within each plot. Geographic area per species pool = 0.2° x 0.2°. Sample sizes per taxonomic distance: 14–75.
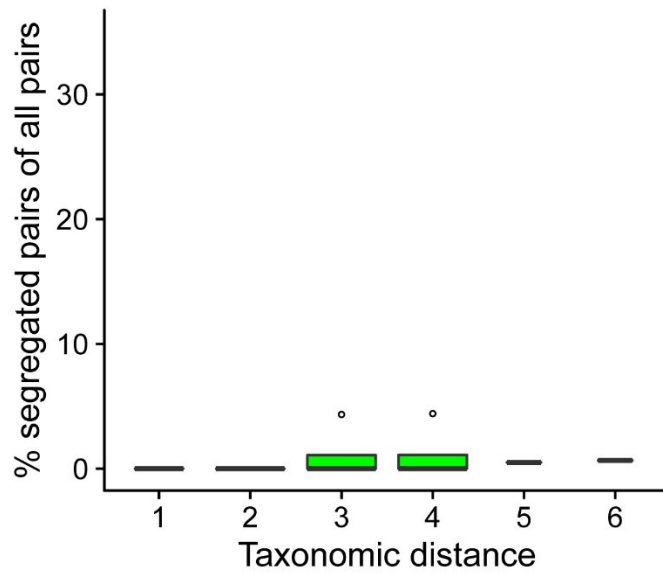
Figure DR6. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the PBDB data using Cambrian Lagerstätten and the stratigraphic scale of beds only. The minimum number of species pairs per data point is 1. Boxplot width is proportional to sample size within each plot. Geographic area per species pool = 0.2° x 0.2°. Sample sizes per taxonomic distance: 1–4.
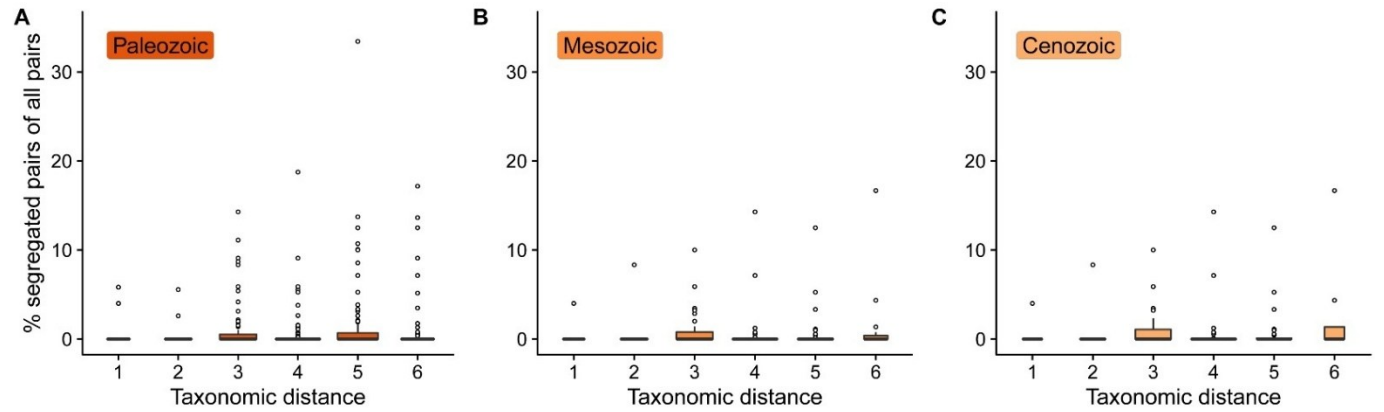
Figure DR7. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance. The minimum number of species pairs per data point is 10. Boxplot width is proportional to sample size within each plot. Geographic area per species pool = 0.2° x 0.2°. A: Paleozoic, sample sizes per taxonomic distance: 9–47. B: Mesozoic, sample sizes: 5–28. C: Cenozoic, sample sizes: 6–29.
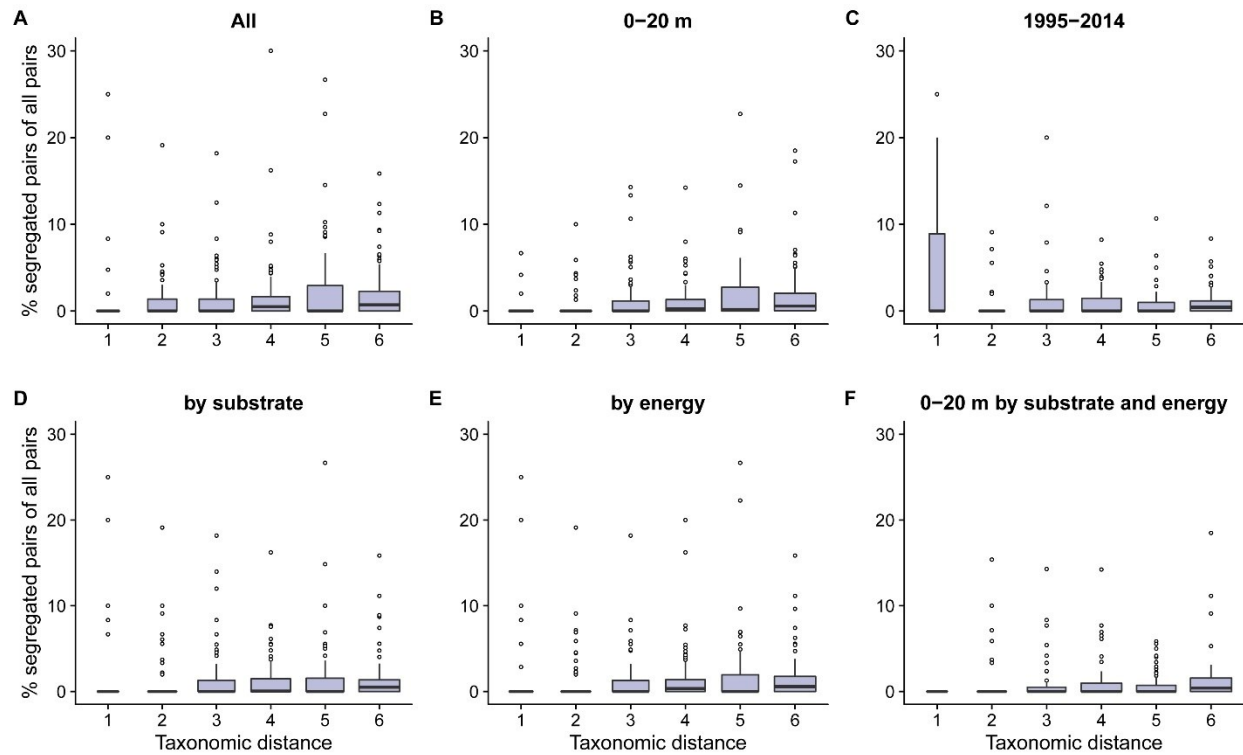
Figure DR8. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the EurOBIS database. Minimum number of species pairs per data point is 10. Geographic area per species pool = 0.2° x 0.2°. One data point represents one species pool. Boxplot width is proportional to amount of data within each plot. A: All data, sample sizes: 41–132. B: 0–20 m depth, sample sizes per taxonomic distance: 30–86. C: 1995–2014, sample sizes: 10–71. D: Data split by substrate, sample sizes: 32–115. E: Data split by energy level, sample sizes: 43–128. F: Data from 0–20 m and split by substrate and energy level, sample sizes: 18–71.
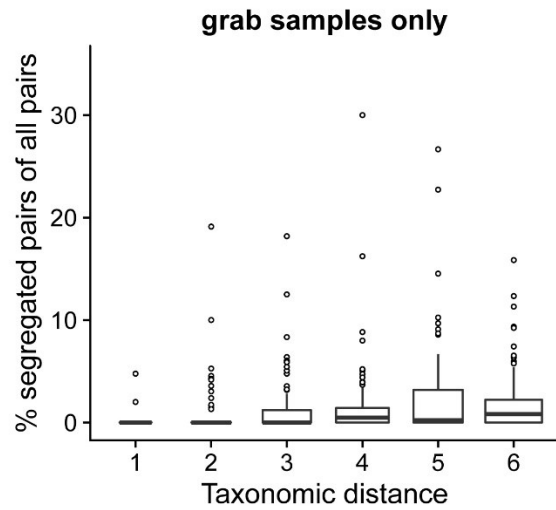
Figure DR9. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the EurOBIS dataset using grab samples only. Geographic area per species pool = 0.2° x 0.2°. The minimum number of species pairs per data point is 10. Boxplot width is proportional to sample size within each plot. One data point represents one species pool. Sample size per taxonomic distance: 38–119.
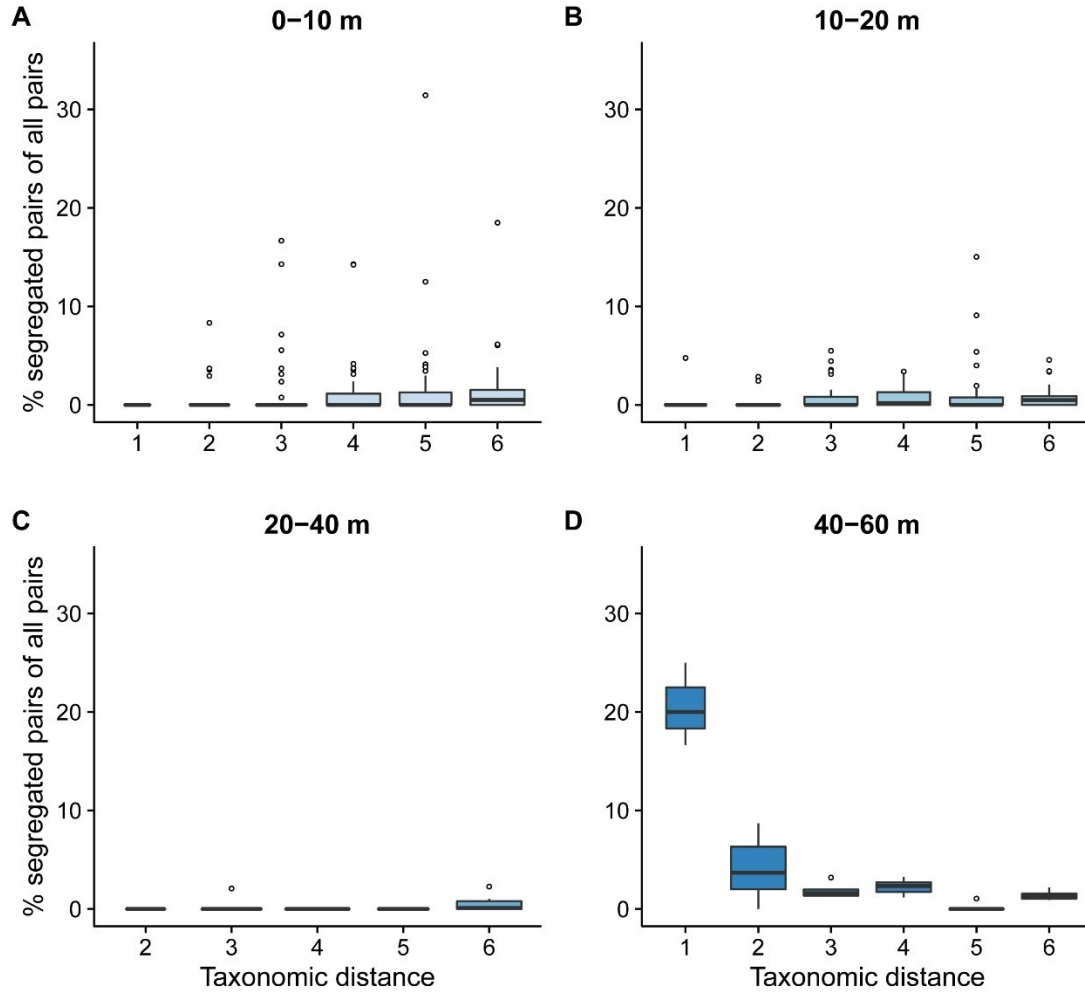
Figure DR10. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the EurOBIS database. Minimum number of species pairs per data point is 5 to increase sample size and the area per dataset is 0.1° x 0.1°. One data point represents one species pool. Boxplot width is proportional to amount of data within each plot. A: Sample sizes per taxonomic distance: 12–51. B: Sample sizes: 20–34. C: Sample sizes: 0–8. D: Sample sizes: 3–6.
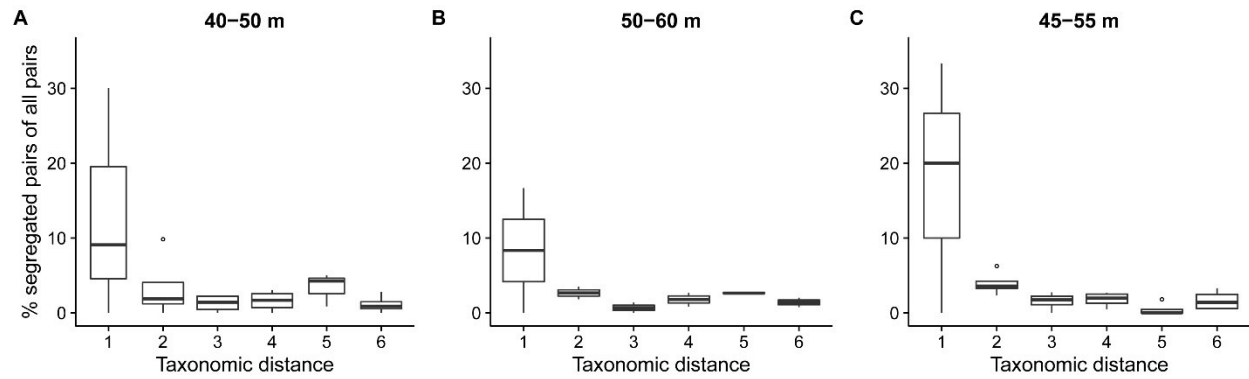
Figure DR11. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for the EurOBIS database for the depth interval yielding elevated levels of segregation among congenerics (Figure 2D). Minimum number of species pairs per data point is 5 to increase sample size and the area per dataset is 0.2° x 0.2°. One data point represents one species pool. A: Sample size per taxonomic distance: 3–4. B: 2 for all distances. C: 3–4.
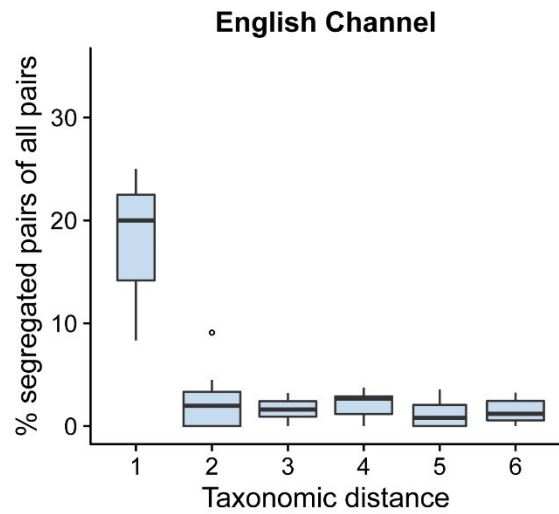
Figure DR12. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for benthos from the English Channel. Minimum number of species pairs per data point is 10 and the area per dataset is 0.2° x 0.2°. One data point represents one species pool.
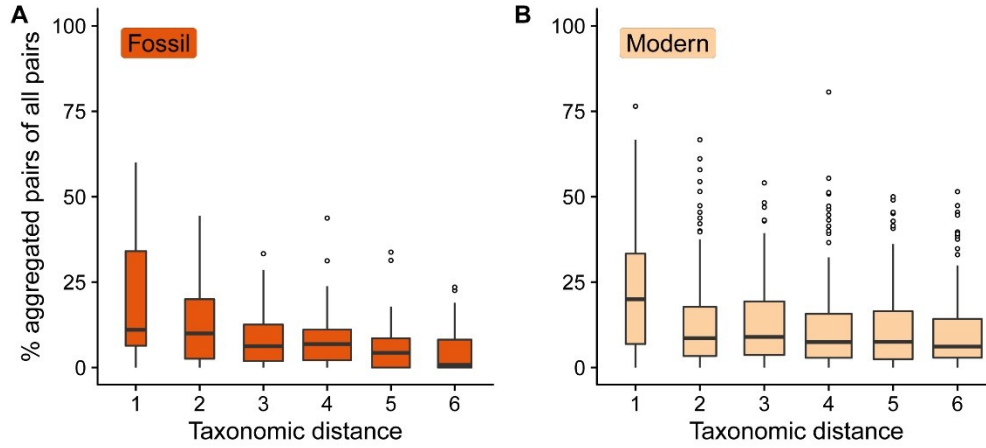
Figure DR13. Boxplots of the percentage of *aggregated* species pairs of all pairs versus taxonomic distance. Minimum number of species pairs per data point is 10 and the area per data set is 0.2° x 0.2°. A: All fossil data with a stratigraphic scale of beds only, sample sizes per taxonomic distance: 14–75. B: All modern data, sample sizes: 47–287.

ADDITIONAL TABLES

Table DR1. Number of species occurrences and the percentages of the five most abundant phyla in each of the databases (prior to defining the minimum number of species and localities per dataset to be analyzed).

	PBDB # species occurrences - top 5	PBDB % species occurrences	EurOBIS # species occurrences - top 5	EurOBIS % species occurrences	EMAPS # species occurrences - top 5	EMAPS % species occurrences
Mollusca	157595	51.5	330529	32.8	25573	22.1
Brachiopoda	49358	16.1				
Arthropoda	29387	9.6	162080	16.1	25743	22.3
Cnidaria	23397	7.6				
Foraminifera	11710	3.8				
Annelida			443685	44.1	60875	52.6
Echinodermata			42949	4.3	1528	1.3
Phoronida			7518	0.7		
Nemertea					689	0.6
totals	271447	88.6	986761	98.0	114408	98.3

Table DR2. Congeneric and confamilial segregated species pairs in the three databases used. A 0.2° latitude x 0.2° longitude area and at least ten species and ten localities/sites per species pool were used. See Appendix DR5 for individual species pairs.

	Congeneric segregated species pairs				Confamilial segregated species pairs			
	Annelida	Arthropoda	Mollusca	Brachiopoda	Annelida	Mollusca	Sipuncula	Porifera
EMAPS	8	1	1		44	2		
EurOBIS	6	3			36	6	1	
PBDB			1	1				1

Appendices DR2–DR4 (.rds data files) can be opened in R using "readRDS("file_name.rds")".

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