

# Multi-scale taxonomic diversity of marine harpacticoids: Does it differ at high and low latitudes?

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**Abstract** We used a comprehensive database comprising a worldwide distribution of 3074 species of marine benthic harpacticoid copepods to explore Arctic (north to 60°N) and tropical (32°S–32°N) faunas. In addition to species and genus richness, we compared the number of observed genera with that expected from a neutral model (random samples from a corresponding species pool). This analysis was performed at three scales: global (Arctic vs. tropics), regional (three Arctic and four tropical regions) and local (78 assemblages). Overall, more than three times as many species and twice as many genera were found in the tropics compared with the Arctic. The number of taxa restricted to a given zone (“climatic endemics”) was much higher in the tropics. All zonal and regional faunas had significantly fewer genera than expected (phylogenetic clumping), but this depletion was more substantial in the Arctic. Phylogenetically, younger families included fewer widely distributed genera and were more species rich at low latitudes, in conformity with the “Out of tropics” hypothesis. At the local level, there was no latitudinal difference in the average species richness. However, the Arctic assemblages

comprised considerably fewer genera than expected, whereas phylogenetic diversity in the tropics only slightly deviated from the expected level. Thus, compared with the tropics, the Arctic harpacticoid fauna shows lower global but similar local species diversity and a lower level of endemicity. The Arctic fauna also shows stronger phylogenetic clumping at all scales, indicating multiple underlying processes of species filtering (evolutionary and ecological).

## Introduction

Explaining the large-scale patterns in biodiversity, such as latitudinal diversity gradients, is among the most important problems in ecology. The causes and drivers of these patterns are still much debated (e.g., Gaston and Blackburn 2000, and references therein). Biodiversity, however, has until recently been measured solely in terms of species (or higher taxa) numbers, with little regard to the phylogenetic aspects, such as the distribution of species within higher taxa. At the same time, phylogeny-based biogeography can be crucial for understanding the processes that determine the contemporary patterns in diversity, including the latitudinal gradients (Wiens and Donoghue 2004).

Since many phylogenetic diversity measures, including the species-to-genera ratio ( $S/G$ ) as the simplest one, are positively correlated with the number of species, one would expect that such measures should trace common patterns in diversity, e.g., latitudinal gradients. However, the actual values of phylogenetic diversity often deviate systematically from the expected level, demonstrating either joint occurrences of related species (high  $S/G$ , phylogenetic clumping) or their segregation (low  $S/G$ , phylogenetic over-dispersion). In particular, Roy et al. (1996) found a significant latitudinal increase in the  $S/G$  ratio for marine

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mollusks along the northeastern Pacific coast, even though the total number of species showed the opposite trend. Similar inverse relationships have also been found for angiosperms (Fenner et al. 1997) and vascular plants in Fennoscandia (Grytnes et al. 2010). Furthermore, Krug et al. (2008) and Harnik et al. (2010) found that the *S/G* ratios for tropical and polar, but not temperate, faunas of marine bivalves lay significantly above the expected level. The counterintuitive latitudinal increase in *S/G* ratios implies phylogenetic clumping at high latitudes, at least at the global and regional levels (local-scale assemblages were not considered). Several hypotheses have been proposed to explain this pattern, involving both large-scale (evolutionary) and local (ecological) forces, but empirical support remains limited, and the cross-scale comparisons are few (Azovsky 1996; Webb et al. 2002; Wiens and Donoghue 2004).

Furthermore, these findings, as many other macroecological studies, are based on macroorganisms, whereas data on global distribution of microscopic metazoans (meiofauna) are extremely scarce. This especially concerns harpacticoid copepods—one of the most diverse groups of marine meiofauna, inhabiting all types of sediments at all depths and latitudes. This group is of particular interest as a test of biogeographical principles, since their typical body size is close to the empirical 1-mm threshold value discriminating macroorganisms with biogeography and microorganisms “without biogeography” (Finlay 2002). Harpacticoids are just the “boundary group” between macro- and microfauna, but their biogeography is poorly known.

Here, we present the first study to compare the diversity of marine benthic harpacticoids from low-latitude (“tropical”) and high-latitude (“Arctic”) shallow waters. More particularly, our null hypothesis was that, at every scale and latitudinal zone considered, harpacticoid taxonomic diversity was statistically indistinguishable from the random subsamples from a larger species pool. Any deviation from the null hypothesis (either phylogenetic clumping or over-dispersion) at a certain scale would indicate some processes of allied species sorting. Furthermore, we hypothesize that difference in the diversity between the high- and low-latitude faunas would indicate the latitudinal variation in the sorting processes.

## Materials and methods

### Data

#### *Global dataset*

A worldwide, taxonomically standardized comprehensive database consisting of spatial occurrences of extant

shallow-water marine benthic harpacticoids was used for the analysis (Chertoprud et al. 2010). The base currently includes the data on 3074 species from 533 genera and contains about 11,000 occurrence records grouped into 35 pre-defined geographical areas. The data were compiled primarily from an exhaustive literature search of over 1000 sources, though some original data were also used. Obligate deep-sea species (only occurring below 300 m) were not considered, since deep-sea harpacticoid fauna is highly specific and largely underexplored (Seifried 2003). While compiling the database, all data passed careful quality control for spelling errors, invalid combinations, synonymy and/or later ascertained misidentifications and were taxonomically standardized using recent revisions and redescriptions. The distribution records from summarizing publications or Web sites were cross-referenced as much as possible with the original papers. Regarding nomenclature, we primarily followed Wells’ (2007) system while accounting for later taxonomic changes and updates.

For the purpose of this study, all Arctic and sub-Arctic regions north of 60°N were considered as the “high-latitude zone.” The areas between 32°N and 32°S were treated as the “low-latitude” or tropical zone. Hereafter, these zones are referred to as “Arctic” and “tropics” for short, even though they also encompass sub-Arctic and subtropical regions, respectively. The fauna of the southern polar regions (Antarctic coasts) was included in the global database but was not analyzed separately because it is insufficiently studied and only a few appropriate local datasets are available (see below). Species and genera were classified according to their distribution across the climate zones. Following Krug et al. (2008), taxa occurred in only one zone (Arctic or tropics) are termed “climatic endemics”; taxa that range extends from tropical to Arctic zones are termed “climatic cosmopolitans.”

#### *Regional datasets*

The Arctic zone was provisionally subdivided into three regions: Central (White and Barents Seas including Spitsbergen), East Arctic (from Kara to Beaufort Sea) and West Arctic (Baffin Bay, Greenland, Iceland and Norway coasts). The tropical zone was further subdivided into four regions: central Atlantic (C\_ATL), Eastern Pacific (E\_PAC) (Americas’ coasts, Polynesia, Hawaii and Galapagos Islands), West Indian (W\_IND) (East Africa coasts, Arabian Gulf and Red Sea) and East Indian–West Pacific (EIWP) (Bengal Gulf, Andaman Sea, South China Sea, Indonesia, Philippines, New Guinea and tropical Australia). At the regional level, the faunas of these regions, retrieved from the global database, were analyzed separately.

### Local datasets

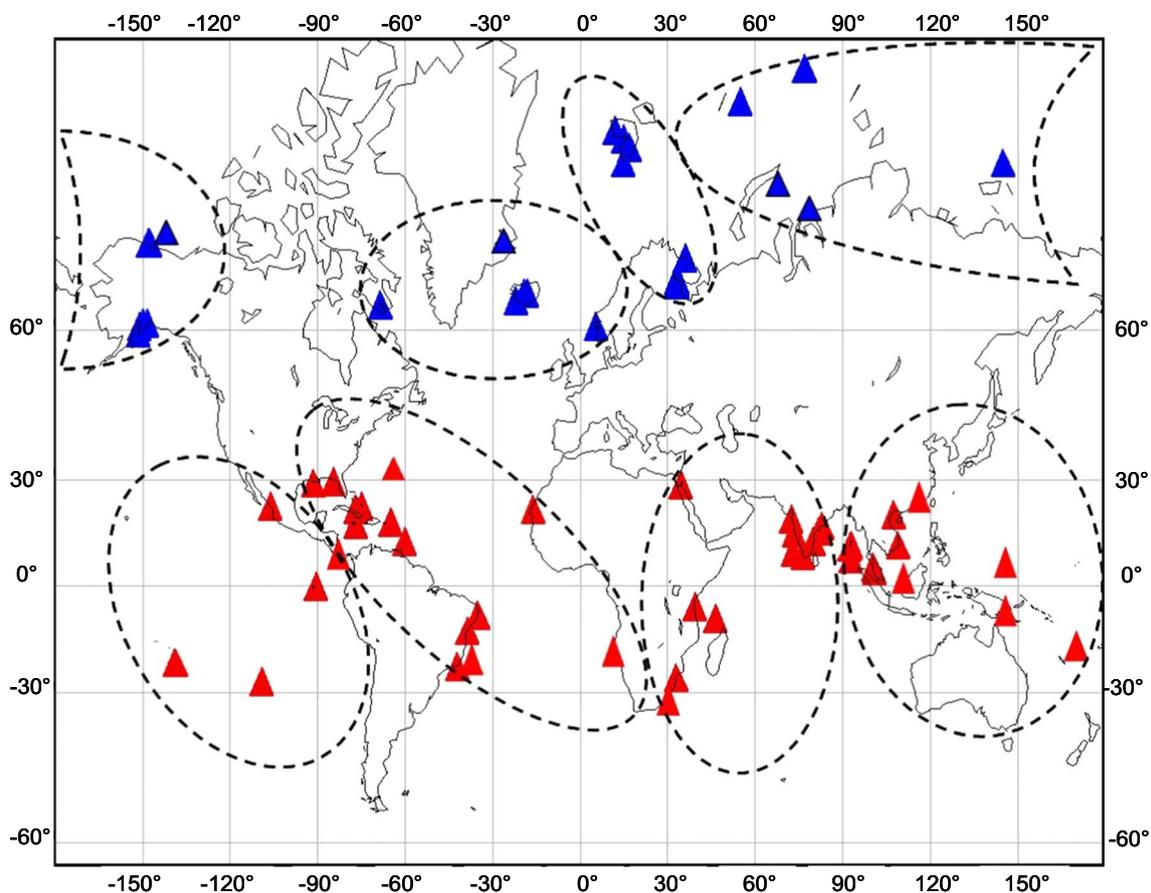
Seventy eight species lists for the local harpacticoid assemblages were compiled from the literature and harmonized according to the modern taxonomy. Faunistic studies based on more or less systematic sampling that explored a wide range of families were mainly chosen; taxonomical studies dealing with particular taxa were also accounted to amend the species lists. Among these local datasets, 29 sites were from the Arctic, and 49 were from the tropics (Fig. 1). The full list of the local datasets with source references is given in Online Resource 1 of the Supporting Information.

The data came from various surveys, which were very different in their scope, design, types of habitats and sampling effort. A more comprehensive survey of various habitats could potentially yield more species in the same genus. To take into account the possible effects of unequal sampling, we estimated the habitat diversity covered by each local dataset. The following habitats were distinguished: silt/mud, sand, gravel/cobbles, fouling of hard substrates (rocks, corals), near-bottom water/ice and macrophytes. Habitat diversity score was estimated as the number of

habitats sampled. If the range of sampled depths exceeded ten meters, one additional point to the score was added to account for bathymetric zonation. Also, the sampling effort was rated as follows: (1) low (short-term local survey with limited number of samples); (2) medium (several sampling sessions in different sites or seasons); and (3) high (extensive long-term survey with large number of samples).

### Phylogeny

The phylogenetic system of Harpacticoida is thus far questionable and is mainly based on morphology, and paleontologic and genetic data are scarce and fragmented and thus not helpful for evaluating the evolutionary age of a taxon. Indeed, the phylogenetic position of many taxa is in a state of flux (Seifried 2003; Boxshall and Halsey 2004). Nevertheless, we decided to use the morphology-based phylogenetic tree to estimate relative age of a taxon (Huys and Boxshall 1991). Based on the most comprehensive phylogenetic scheme proposed by Seifried (2003), we assessed three families of the most plesiomorphic clades: Polyarthra (comprising Longipediidae and Canuellidae) and



**Fig. 1** Map of local datasets used for the analysis (triangles). Dashed lines show approximate boundaries of the regions (see text for details)

Aegisthoidea (Aegisthidae)—as the “oldest” ones; the “relatively old” families included Neobryidae, Ectinosomatidae and all representatives of the Podogenonta lineage, while later diverged Exanechentera members (Peltidiidae, Porcellidiidae, Tegastidae, Tisbidae, Novocriniidae, Paramesochridae, Superornatiremidae and Tachidiidae) were treated as “young” families.

### Statistical analysis

The species-to-genera ratio ( $S/G$ ) is often used as the simplest measure of phylogenetic diversity. Proposed as early as 1901 by the plant biogeographer Paul Jaccard, this ratio was used to identify emergent patterns in the structure of assemblages by, for example, directly relating its to the intensity of interspecific competition. However, this approach has been criticized repeatedly because the  $S/G$  ratio depends strongly on the species number and is thus not directly comparable between datasets acquired through variable and unknown sampling effort (see Azovsky 1996 for historical review). To overcome this pitfall, observed  $S/G$  values should be adjusted to the null expectation by applying the appropriate neutral model (Simberloff 1970; Azovsky 1996; Webb et al. 2002). In addition, such comparison does not imply any testable null hypothesis.

Therefore, we assessed taxonomic diversity against a null model derived from a randomization of the appropriate species pool. The implicit null hypothesis is that the taxonomic structure of a given species list is not distinguishable from a random sample from the species pool containing it. The model was obtained by randomly drawing species (without replacement) from a corresponding species pool (a “master list”), assuming that the species arrived randomly and independently into the sample from the pool. Given the number of species in a sample and the taxonomic composition of the master list, this null model represents the expected mean number of genera ( $G_{exp}$ ) in that sample. The standard deviation (SD) for  $G_{exp}$  was also estimated by resampling. The  $G_{exp}$  and SD calculations were

performed by applying the individual rarefaction procedure in the PAST software version 3.04 (Hammer et al. 2001).

We then compared the observed ( $G_{obs}$ ) and expected genus numbers using the standardized effect size of genera (SESG), which was calculated as the difference between the observed and expected numbers of genera, divided by the SD of the expected value:  $SESG = (G_{obs} - G_{exp})/SD$ . The SESG ranges from negative to positive infinity; positive values represent over-dispersion (when the species list includes more genera, i.e., fewer congeners, and has a lower  $S/G$  ratio than expected), whereas negative values represent under-dispersion (a list composed of species that are more related than those of a null model).

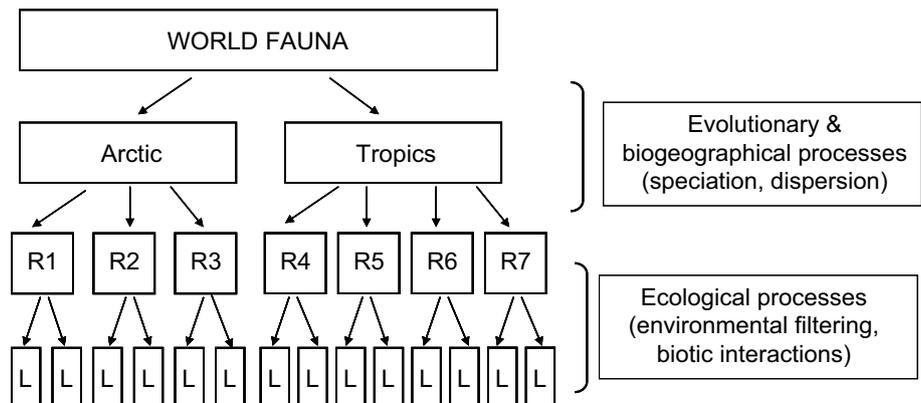
The use of SESG has many advantages. First, this estimator is robust to varying richness and uncontrolled sampling efforts and is thus comparable across various datasets (Fenner et al. 1997; Krug et al. 2008; Grytnes et al. 2010). Second, because its values are standardized relative to the expected distribution, SESG directly indicates the strength of deviation from neutrality. Values between 2 and  $-2$  indicate that the taxonomic diversity deviates insignificantly from a random sample (i.e., the observed number of genera lies within a 95 % CI for the expected level), whereas values beyond this range indicate sufficient deviation.

This analysis was sequentially performed at three levels (Fig. 2):

1. A global comparison was performed for the Arctic and tropical datasets using the entire fauna (3074 species) as the “master list”;
2. A regional-to-global comparison was performed for each of seven regional datasets, with the Arctic or tropical fauna as the corresponding “master list”;
3. A local-to-regional comparison was performed for 78 local datasets, with the corresponding regional fauna as the “master list.”

A nonparametric Mann–Whitney test and a paired Wilcoxon test for equal medians were used for the

**Fig. 2** Data design (*left*) and presumptive underlying processes affecting phylogenetic diversity (*right*). Regional and local datasets are marked as *R* and *L*, respectively. Overlying dataset is used as a species pool (“master list”) for the underlying datasets



Arctic–tropics comparisons. To check the difference in the SESG values between regions, a Kruskal–Wallis multiple-group test was used with sequential Bonferroni correction of *p* values for multiple comparisons. We also performed nonparametric analysis (PERMANOVA) to test the effects of sampling effort, habitat diversity and latitude on local species richness and SESG values.

Additionally, the “average taxonomic distinctness” (AvTD,  $\Delta^+$ ) was estimated for the regional datasets to assess whether the observed  $\Delta^+$  values are consistent with a random distribution model (i.e., assuming that the species distribution is taxonomy independent). We performed the randomization test ( $N = 1000$ ) available in PRIMER v. 6.0 (Clarke and Gorley 2006) to estimate the 95 % probability limits for the  $\Delta^+$  values.

## Results

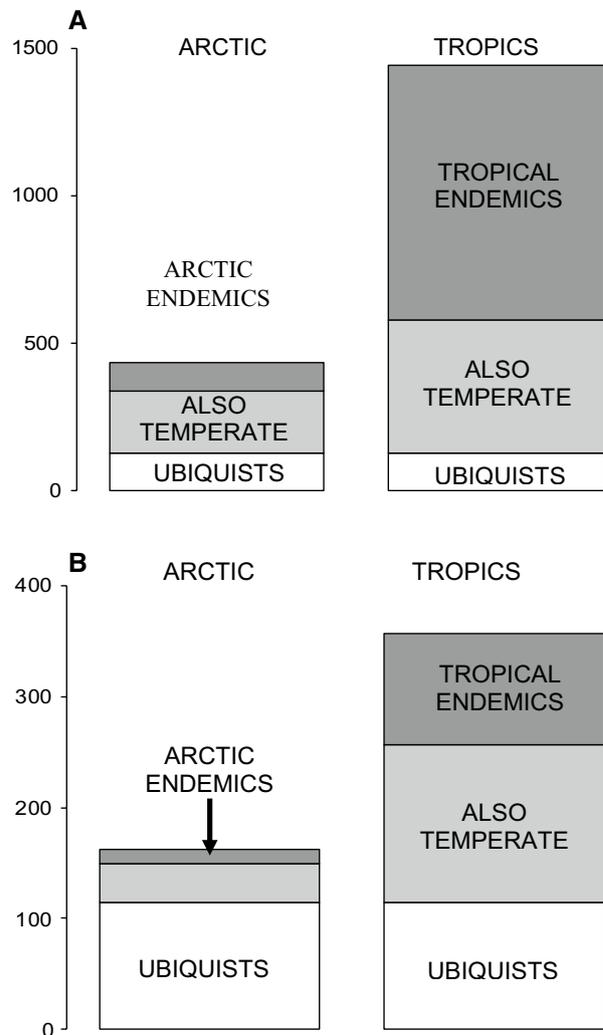
### Global diversity

Overall, 433 species (162 genera) have been reported from arctic shallow waters, and only a minor subset of these (96 species and 13 genera) are found exclusively in this zone and could thus be treated as potential “arctic endemics” (Fig. 3). More than three times as many species (1442) and twice as many genera (358) are found in the tropics. Among them, 91.6 % of “tropical” species and 68.0 % of genera are not present in the Arctic, and 60.1 % of these species (28.1 % of genera) are limited to the tropical zone in their distribution (“tropical climatic endemics”).

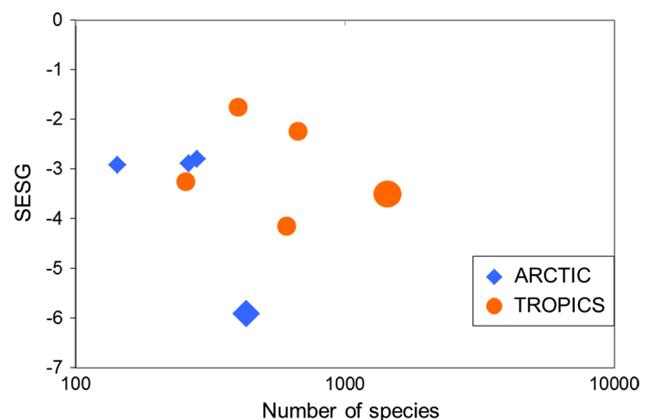
A total of 126 species and 115 genera have been recorded from the Arctic to the tropics (“climatic cosmopolitans”). In addition, 15 species and eight genera occur both in the Arctic and in anti-boreal zone and/or the Antarctic but not in the tropics. These taxa either have a bipolar distribution or may be potential cosmopolitans.

Thus, the tropical fauna of harpacticoids, considered as a whole, appears to be much richer and more specific than that of Arctic zone (Fig. 3). In addition, the tropical fauna has a higher *S/G* ratio (4.03 vs. 2.67 in the Arctic). When compared with the null model, however, we obtained an SESG value equal to  $-5.91$  for the Arctic and  $-3.29$  for the tropics. Both values (the large symbols in Fig. 4) are far beyond the  $\pm 2$  band (95 % CI for the null model), indicating significantly fewer genera (higher *S/G* ratios) than expected. This depletion (“phylogenetic clumping”) is notably more substantial in the Arctic region.

Additionally, we separately compared the average species richness for the genera with a different type of distribution. The cosmopolitan genera comprised significantly more species in the tropics than in the Arctic, and the endemic genera had on average many fewer species than



**Fig. 3** Composition of Arctic (left histogram bar) and tropical (right bar) fauna according to the “global” dataset: number of species (a) and genera (b) with different distribution ranges. Climatic cosmopolitans are designated as “ubiquists”



**Fig. 4** Standardized genus richness (SESG values) for zonal (Arctic and tropics, large symbols) and regional (small symbols) datasets

the widely distributed genera, both in the Arctic and in the tropics (Table 1).

### Species richness and phylogenetic age of families

Phylogenetically, ancient clades were better represented in high latitudes than the recent ones. Percent of species presented in the Arctic fauna, decreased regularly from 21 % in the “oldest” families to 7 % in the “young” families (Fig. 5). In the tropics, all age groups were more or less equally represented, each having 50–60 % of its total richness. The “oldest” families comprised on average 10.7 species in the Arctic compared with 31.3 species in the tropics. Similar figures were observed for other “relatively old” families: 10.6 and 32.5 species, respectively. In contrast, the “young” families comprised only 4.6 species in the Arctic compared with 35.1 species in the tropics. Furthermore, an average 46.5 % of genera in the “oldest” families were climatic cosmopolitans, i.e., had representatives in all climatic zones, whereas only 20.4 % genera in the “young” families were cosmopolitans. In other words, phylogenetically older taxa were more successful in settling the Arctic zone, whereas younger taxa were more restricted to the tropics in their distribution.

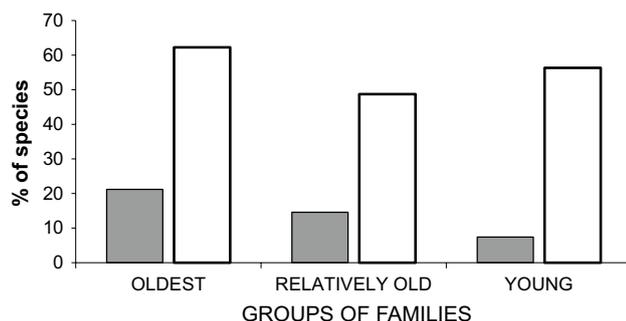
### Regional diversity

Some 55 % of the Arctic species were found in only one region; this value was much higher (76.5 %) in the tropics.

**Table 1** Species-to-genera ratios for “climatic endemic” and “climatic cosmopolite” genera

	High latitudes	Low latitudes	<i>p</i> value
Cosmopolites	3.10 ± 3.15	7.02 ± 7.46	10 <sup>-5**</sup>
Endemics	1.15 ± 0.38	1.55 ± 1.08	0.164*
<i>p</i> value	0.0031*	10 <sup>-7*</sup>	

Mean *S/G* ratios and SD are given in the upper-left cells; *p* values for corresponding pair-wise comparisons are shown in the lower-right marginal cells (\* Mann–Whitney test; \*\* paired Wilcoxon test)



**Fig. 5** Percent of species belonging to families of different ages, presented at Arctic (gray bars) and tropical (white bars) faunas

With regard to genera, these values were almost identical (44.4 and 43.6 %). Thus, the Arctic fauna demonstrated lower regional endemism at the species level but not at the genus level.

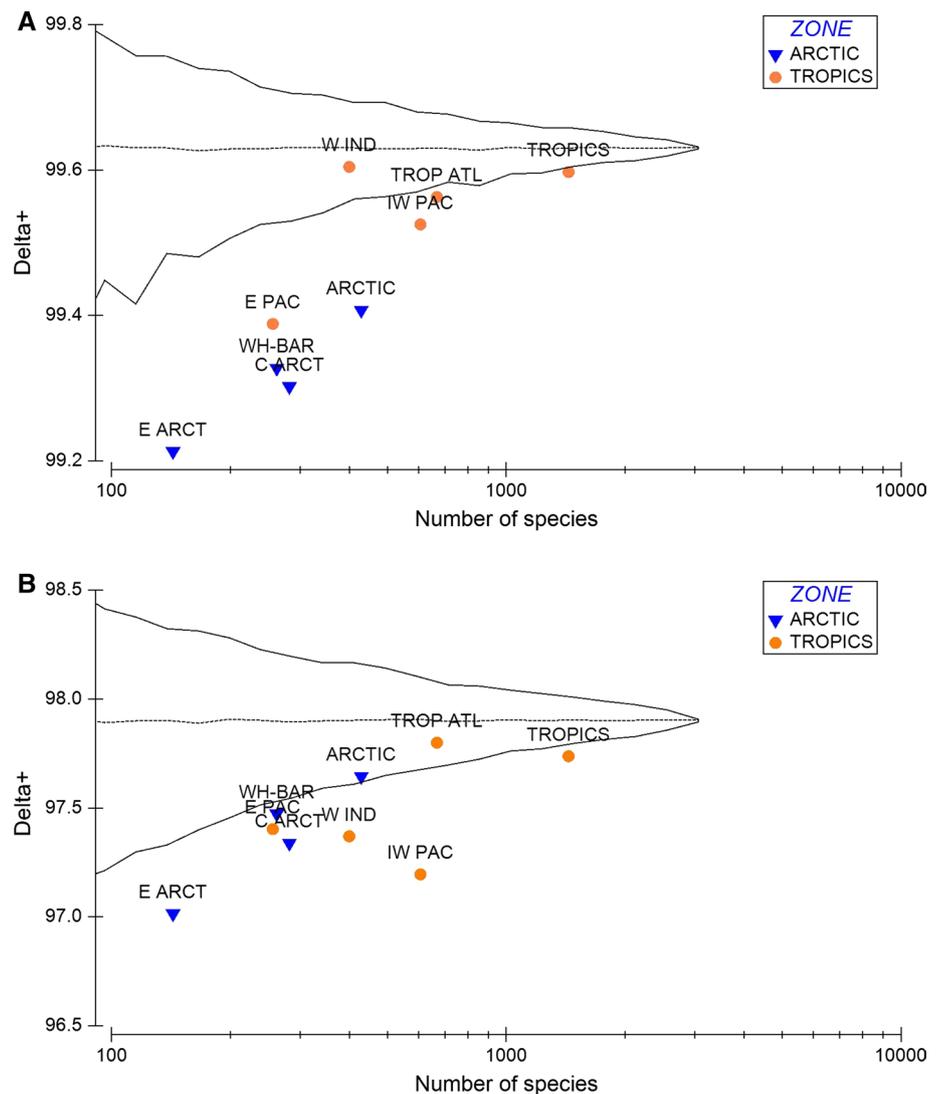
All three arctic regions have sufficiently lower negative SESG values than expected for random samples from Arctic fauna. This is also true for all tropical regions except the West Indian region (Fig. 4). Thus, almost all regional faunas consistently indicate “phylogenetic clumping” of species that constitute the zonal pools. The average taxonomic distinctness ( $\Delta^+$ ) calculated up to the genus level (i.e., ignoring the grouping of genera by families, Fig. 6a) showed a pattern that was consistent with that of SESG. The Arctic fauna showed more pronounced declines in taxonomic diversity than the tropical fauna. The same procedure was applied for the full taxonomic range (accounting for the assignment of both species to genera and genera to families), and similar results were observed (Fig. 6b): all regions but one (tropical Atlantic) showed lower phylogenetic diversity than expected, though the difference between low and high latitudes became negligible.

### Local diversity

Sampling effort turned to be the main factor influencing the local species richness (Fig. 7a). As expected, the more extensive surveys yielded more species (PERMANOVA test:  $p < 10^{-16}$ ). Local richness also slightly increased if several habitat types were investigated ( $p = 0.065$ ), while the difference between low- and high-latitude localities was insignificant (Fig. 7a, b). On average, the Arctic localities included 48.2 species, and the tropical localities included almost the same number (46.4 species). The three outliers with unusually high species diversity were Kandalaksha Bay (the White Sea, 168 species), Inhaca Island near Mozambique (126 species) and the Andaman Islands in the Indian Ocean (119 species), the three sites of long-term systematic studies. Except for these three sites, the majority of localities exhibited from 30 to 50 species each, regardless of location.

Finally, we tested the genus diversity of local assemblages, comparing it with the expected values for random draws from the respective regional species pools. Neither sampling effort nor habitat diversity had any effect on SESG values (PERMANOVA tests:  $p = 0.33$  and  $0.14$ , correspondingly). It provides some assurance that further analysis was not affected by an inherent sampling bias (Fig. 7 c, d). The difference between high and low latitudes, however, was highly significant. Most of the tropical assemblages (41 out of 49) had SESG values within the 95 % scatter band of the null model, and only eight points showed significantly negative values (Fig. 8). In contrast, all Arctic communities strongly deviated from neutrality, again having fewer

**Fig. 6** Average taxonomic distinctness ( $\Delta^+$ ) calculated up to genera level (a) and up to family level (b). A funnels represent the 95 % limits for a random draws from the World fauna master list. See “Materials and methods” for the regions’ abbreviations



genera but more congeners than expected. The Mann–Whitney pairwise *post hoc* test confirmed a highly significant difference in SESG between the Arctic and tropical datasets, though differences between the tropical regions were insignificant (Table 2). Thus, there was a pronounced difference in phylogenetic diversity between high and low latitudes, even at the level of local assemblages.

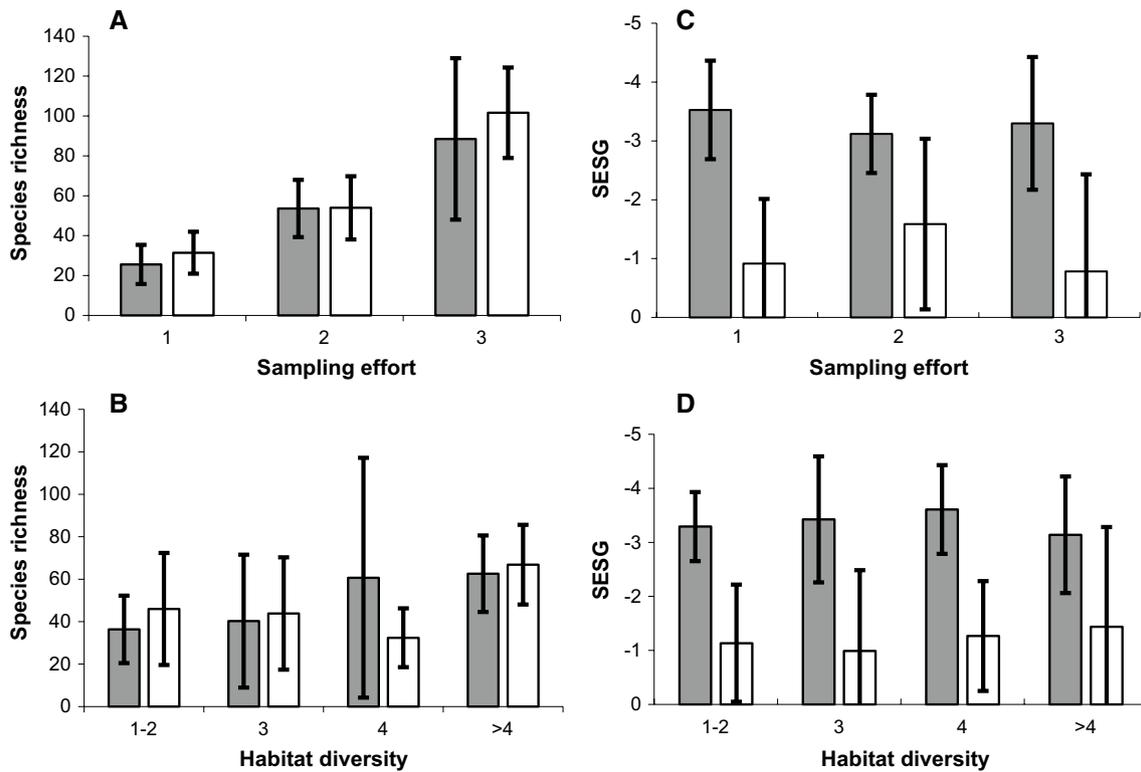
## Discussion

We have analyzed diversity of marine benthic harpacticoids at three levels: global (high and low-latitude bands entirely), regional (on spatial scale of  $10^3$ – $10^4$  km) and local (assemblages from confined areas, on scale of  $1$ – $10^2$  km). The analysis reveals noticeable latitudinal differences in all considered aspects of diversity, i.e., in species and genera richness, endemism and species-to-genera

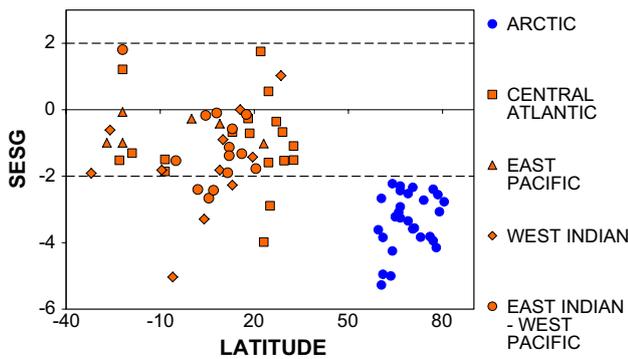
ratio. Below we discuss these differences, with special attention to spatial scale of their manifestation.

### Patterns in species and genus richness

There are three times as many harpacticoid species and twice as many genera in the tropics than in the Arctic. However, there is no difference in local richness between tropical and arctic localities. On the other hand, the local richness strongly correlates with diversity of habitats, indicating the prominent role of spatial heterogeneity. This is in good agreement with our previous findings that marine harpacticoids show a latitudinal trend in spatial turnover (beta diversity) but not in alpha diversity (Azovsky et al. 2012). Recently, Fonseca and Netto (2014) analyzed data for nematodes from 43 estuaries around the world and found that genus turnover decreased with increasing latitude, whereas local genus richness did not show a clear latitudinal trend. Similar latitudinal changes



**Fig. 7** Mean values of local species richness (a, b) and standardized genus richness (SESG) (c, d) for datasets of various sampling effort (a, c) and habitat diversity (b, d). Gray bars are mean values for Arctic data, white bars for tropics; vertical lines are SD



**Fig. 8** Standardized number of genera (SESG) values for the local datasets plotted against latitude. Data for different tropical regions are shown by different symbols. Dashed lines show the 95 % confidence range for neutral model

in species turnover but not in local diversity have also been reported for some other marine and terrestrial groups (see Azovsky et al. (2012) for additional references and Soinen et al. (2007) for an extensive meta-analysis). All these findings allowed us to consider spatial turnover (beta diversity) as the crucial component in forming a global latitudinal diversity gradients, while local richness seems to be driven by another set of factors.

**Table 2** Mann–Whitney pair-wise post hoc tests for Arctic and four tropical sets of SESG values (abbreviations see “Materials and methods”)

	C_ATL	W_IND	EIWP	E_PAC
ARCTIC	<b>0.0002</b>	<b>0.0052</b>	<b>9.816E-06</b>	<b>0.0016</b>
C_ATL		0.6058	0.6527	0.2613
W_IND			0.7164	0.2671
EIWP				0.1471

Raw *p* values are shown; the significance is estimated after sequential Bonferroni correction for multiple comparisons. The significant differences are given in bold

Meanwhile, the above-mentioned difference in total harpacticoid richness may be partially caused by the insufficient exploration of polar fauna. The unequal number of the appropriate datasets (29 polar vs. 49 from tropics) indirectly confirms such insufficiency.

**Patterns in climatic endemism**

Taxa with wide and restricted climatic ranges show sharply asymmetric distributions between high and low latitudes. Indeed, only 22 % of species and 8 % of genera recorded at high latitudes are potential endemic to this zone, whereas

these figures are notably higher in the tropics: 60 % of endemic species and 28 % of genera. Eleven of 13 polar endemic genera are monotypic, though one-third of “tropical endemic” genera include several species. It was shown earlier that percent of endemic harpacticoids tended to be lower at high latitudes, even after correction for species richness (=sampling effort) (Chertoprud et al. 2010). This type of asymmetry in the distribution of climatic endemics is not a specific feature of harpacticoids. Similar pattern, known as Rapoport’s rule (Stevens 1989), has been demonstrated repeatedly for large metazoans (Gaston and Blackburn 2000; Ruggiero and Werenkraut 2007). Our findings allow the extension of this rule to small-sized meiofauna as well, whereas some protists, e.g., ciliates, show the reversed pattern (Azovsky and Mazei 2013).

### Patterns in the $S/G$ ratio

Perhaps the most intriguing and counterintuitive results were observed for the species-to-genera ratio. It would be natural to expect more species per genus in the tropics, area that is commonly assumed to have higher diversity and high speciation rates. However, we obtained quite the opposite: on the whole, the higher than expected  $S/G$  ratios (i.e., negative SESG values) were observed at high latitudes despite the low number of taxa at that zone. This difference is observed at both global and regional levels but is most clearly pronounced for the local-scale data (compare Figs. 4, 8). As mentioned in the Introduction section, similar results have also been reported for some other groups.

Several hypotheses could be proposed to explain these patterns.

1. Null hypothesis: this pattern is an artifact of data selection, sampling or identification biases, or “distribution of taxonomists.” All the species lists, however, had been processed using the same checking and unification procedure to ensure their accordance with recent taxonomical revisions (see the “Materials and methods” section). Our analysis shows that neither sampling effort nor habitat diversity has significant effect on SESG values. Also, there are no reasons to suggest that more taxonomists “splitters” worked in the Arctic than in the tropics, and any “latitudinal” difference in their experience level is also doubtful. Nevertheless, for greater assurance, we performed an additional “pair-wise test” comparing Arctic versus tropical datasets reported by the same authors (or at least with the participation of the same authors). We found eight such pairs, and the SESG values were significantly lower for the Arctic datasets compared with their tropical “counterparts” (paired Wilcoxon test:  $p = 0.0078$ ,  $n = 8$ ).

Thus, there is no evidence supporting the null hypothesis.

2. The higher than expected  $S/G$  ratios near the pole might have resulted from relatively high net rates of speciation: the few lineages that manage to reach this zone are free to diversify there, producing more species per lineage than expected (the high-latitude diversification hypothesis, see Weir and Schluter 2007; Krug et al. 2008). However, this hypothesis is not supported by our data. There are precious few endemics at high latitudes (Fig. 1), and endemic genera in the Arctic have lower  $S/G$  ratios than those in the tropics (Table 1) (11 of 13 high-latitude endemic genera are monotypic, and all belong to the “old” families). Cosmopolitan genera have several more species, but they also tend to decline in species richness at high latitudes. These latitudinal differences in  $S/G$  ratios were most pronounced in the “young,” phylogenetically advanced families. Therefore, the higher than expected  $S/G$  ratios at polar zone are driven by genus depletion rather than by rapid diversification.
3. “Out of tropics” hypothesis, or “equatorial pump” acting at the genus level. The low-latitude zone is considered the point of origin for many higher taxa that subsequently disperse polarward, though this dispersal is delayed and selective. This assumption, first made by Darlington (1957) and Meyen (1987) under the name of “equatorial pump,” was later developed and proved by Jablonski et al. (2006, 2013) as the mechanism of latitudinal diversity gradient formation (the “Out of tropics” hypothesis). Taking into consideration the high tropical origination rates and low polar extinction rates, this model treats polar diversity as a result of the accumulation of taxa that evolved elsewhere in the world (preferentially in the tropics) and then expanded their ranges poleward (Jablonski et al. 2006; Krug et al. 2008). The low total diversity of Arctic fauna indicates that not every taxon was able to pass through the climatic and geographical filters. If these successfully expanding taxa primarily belong to older and usually species-rich clades, this scenario should generally lead to higher  $S/G$  ratios at high latitudes than for rapidly diversifying, highly endemic tropical fauna.

Our results are consistent with this hypothesis. First, a lower percentage of endemics were found in the Arctic (both at the species and at genus levels, Fig. 3). Second, young families were the poorly represented in the Arctic and showed no endemic genera there, likely because they have had too little time for expansion and/or divergence. Third, it is the tendency for genera with large latitudinal ranges to be more species rich within each climatic zone

(Table 1). Thus, those genera that reach the poles are not a random subset of the global biota.

Therefore, the global-level pattern agrees well with the “Out of tropics” model. However, this model appeals to evolutionary processes (i.e., speciation, extinction and range expansion) operating at large spatiotemporal scales, and thus, it is inapplicable to local-scale diversity patterns (Swenson 2011, Buschke et al. 2014). Our analysis reveals that Arctic and tropical assemblages do not differ in their average species richness (Fig. 7a, b); however, the Arctic assemblages are not simply an equivalent proportion of the regional diversity: they have significantly higher *S/G* ratios than expected (phylogenetic clumping, see Fig. 8; Table 2). This result was obtained by a comparison with random subsets from respective regional species pools and thus was exempted from global- and regional-level effects. Therefore, some additional, *community-level* mechanisms of ecological sorting should be suggested to explain this pattern.

Recently, Arita et al. (2014) applied a similar approach to analyze New World bats. They reported fewer genera than expected at high latitudes, whereas these figures were close to or slightly higher than expected in the tropics—the pattern similar to our “local-scale” one. Arita et al. grouped the data into one-degree latitudinal bins (approximately 111 km), a scale that is intermediate between our “local” and “regional” scales, but corresponding more closely to the local scale if accounting for the higher dispersal rate for bats than for benthic harpacticoids.

Ecological theory has yielded two main types of these sorting mechanisms:

1. Competitive exclusion: closely related species, being also more similar ecologically, should compete most severely and thus should coexist more rarely than taxonomically distant ones, resulting in phylogenetic overdispersion;
2. Environmental filtering: closely related species with similar environmental preferences should co-occur more often in the same habitats, which should result in phylogenetic clustering.

Both mechanisms imply that more closely related species tend to show more similar ecological features than expected by chance (phylogenetic niche conservatism). In fact, both mechanisms can act simultaneously but are expected to have opposing effects; thus, the observed phylogenetic community pattern is a result of a balance between the two processes (Cavender-Bares et al. 2009; Mayfield and Levine 2010). A number of studies on various groups evidence that this balance depends on the spatial scale, taxonomic resolution and environmental heterogeneity (Azovsky 1992, 1996; Cavender-Bares et al. 2006,

2009; Stevens et al. 2011; Swenson 2011). Moreover, at certain scale the effects of these processes may compensate for each other, such that the resulting pattern becomes indistinguishable from the neutral model expectation (null balance, Azovsky 1996).

The results presented herein reveal the obvious latitudinal shift in this balance, with strong phylogenetic clumping at high latitudes. Within the aforementioned theoretical framework, two additional hypotheses can be proffered to explain this difference:

4. Arctic communities face more severe environmental filtering than tropical ones;
- and/or
5. There is more severe competition in the tropics, which more frequently leads to local exclusion of relatives.

Our data do not allow us to prefer either (or both) of these hypotheses. More generally, both possibilities (i.e., latitudinal shifts in environmental filtering or in the strength of biotic interactions) have been discussed, but direct evidence is scarce and controversial. Tropical environments are widely assumed to be highly diversified, providing a greater variety of resources and thus more possibilities for fine niche specialization (Rohde 1978; Dyer et al. 2007; but see Beaver 1979; Novotny et al. 2006; Lewinsohn and Roslin 2008 for counter-evidence). Qiao et al. (2015) analyzed species abundance distribution data for 32 forest tree communities and found that the deviation from neutrality correlated with latitude; they interpreted this as an indication of an increase in the strength of environmental filtering in regions further from the tropics. Similarly, latitudinal differences in competition intensity are often assumed to be important (e.g., Luiselli 2006), but the evidence for this claim is again rare and ambiguous. Recent work synthesizing studies of marine sessile benthos (Barnes 2002; Barnes and Kukliński 2003) has suggested that interspecific competition at low latitudes is more frequent but less frequently leads to competitive exclusion. Notably, in their extensive review, Schemske et al. (2009) failed to offer any direct comparisons of the strength of interspecific competition across latitudes.

There are some evidences that local meiobenthic diversity is mainly driven by local environmental conditions, rather than by latitude (harpacticoids: Rybnikov et al. 2003; Azovsky et al. 2012, and the present study; nematodes: Mokievsky and Azovsky 2002; Fonseca and Netto 2014). So we prefer the environmental filtering as the most likely mechanism of local-scale phylogenetic clumping. Deeper studies are necessary, however, to make a reasonable judgment.

## Conclusion

Our analysis reveals that the phylogenetic diversity of marine benthic harpacticoids is non-randomly filtered at all levels: zonal (i.e., high vs. low latitudes as a whole), regional and local. The signals of phylogenetic clumping are stronger at high (Arctic) latitudes. At zonal and regional levels, this difference could be explained within the framework of the “Out of tropics” model. The most obvious contrast between latitudes, however, appears at the local scale, indicating also the difference in some community-level mechanisms of species sorting. These results confirm that biodiversity is nested hierarchically across spatial scales (Buschke et al. 2014). The observed patterns in biodiversity, including latitudinal gradients, are therefore the result of multiple underlying evolutionary and ecological processes. Decomposing their effects and quantifying their relative roles would perhaps be more fruitful, rather than searching for a simple single-factor explanation unified across taxa, scales and regions. In particular, studies exploring biogeographical variations in local ecological processes are the next logical step toward this goal.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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