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The Role of Old Relicts in Structuring the Boreal/Tropical Transitional Zone: The Case of East Asian Planktonic Cladocera (Crustacea)

Ivan I. Krolenko , Petr G. Garibian and Alexey A. Kotov * 

A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninsky Prospect 33, Moscow 119071, Russia

* Correspondence: alexey-a-kotov@yandex.ru

Abstract: Previous studies provided evidence of the mixing of boreal–tropical cladocerans (Crustacea) in the Far East of Eurasia, as well as the presence of numerous pre-Pleistocene relict endemics. In this study, we hypothesize that the colonization history is reflected in the proportions of endemic/boreal/tropical taxa among different habitat types within this region. We analyzed 442 qualitative samples collected from seven sub-regions of the Far East of Russia and South Korea along a latitudinal transect of approximately 2200 km, where we identified 101 Cladocera species. Our results showed a significantly higher proportion of endemic taxa in the plankton compared to the littoral and benthic zones. The proportions of endemic/boreal/tropical taxa in the permanent and temporary waters were similar. We observed a distinct shift in dominance in benthos and littoral zone across our transect: boreal taxa were prevalent in the northern sub-regions (1–4), while tropical taxa were prevalent in the southern sub-regions (5–7), with a pronounced boreal–tropical transition zone (sub-regions 4–5). Our findings suggest that this pattern arose due to the unhindered dispersion of the two faunas in a latitudinal direction until they met at the boundary during their arrival in the Late Pleistocene. In contrast, the proportions of the boreal and tropical taxa in plankton did not exceed 16% in any of the studied sub-regions, and the proportion of boreal taxa decreased from 16% to 10%, while that of the tropical taxa increased from 0% to 10% from north to south. We propose that the lower proportions and the absence of mixing of fauna in the plankton can be explained by the strong presence (sometimes dominance) of relicts that occupy these water bodies before the arrival of colonizers from the north and south. Our findings highlight the significant role of biotic interactions in the formation of biogeographic boundaries, which was previously underestimated.

Keywords: zoogeography; Far East; zooplankton; continental waters

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1. Introduction

Interest in the biodiversity of continental water bodies is continuously increasing as global climatic change and other anthropogenic threats grow. Regions of particular interest are “biogeographic ecotones,” the transitions of biogeographic zones with mixing of regional faunas [1–8]. The Palaearctic/Oriental boundary is such a zone, but authors have differed as to the locations of the boundaries [3,9–12]. For freshwater, the differentiation between the Palaearctic and Oriental zones (concerning Korea, Japan, and the Amur basin) is particularly pronounced [9,13–15].

Water fleas (Crustacea: Cladocera) are present in the continental water bodies of different types; they frequently dominate among planktonic animals [16,17]. This is a relatively diverse (c.a. 300 species in Northern Eurasia [18]) group, differentiated as early as the Paleozoic [18,19]. The resting eggs of the Cladocera are easily dispersed by wind (in arid regions), water currents, and, in particular, by water birds [20,21]. They are regarded as a model group for ecology, evolution, and toxicology [22,23], and as indicators of water quality [24], the tropic status of lakes [25], fish pressure on planktonic communities [26], etc.

Their remains are well-preserved in the lake bottom sediments, and they are widely applied in the paleoecological reconstructions [27–30].

Cladocera is also a model aquatic group for the biogeography of the Far East. Recently, there has been an increase in faunistic and taxonomic studies of cladocerans in this region. Researchers have published new checklists for South Korea [31] and China [32,33], as well as conducting analyses of the Russian Far East [34–36]. These studies have shown that tropical taxa have been able to penetrate deep into the north of the region, reaching as far as the central portion of the Korean Peninsula [31,37–39], as well as the Primorsky Krai, Amur, and Khabarovsk areas of Russia [34,40–44].

Kotov [35] subdivided all the cladoceran taxa in northeast Asia into several faunistic complexes, which are groups of species with similar, or sometimes different, recent geographic distributions, but with similar centers of differentiation and dispersion in the past. The four faunistic complexes identified in the Far East are:

1. Widely distributed Eurasian (WE).
2. Widely distributed in East Asia and North America (EAA).
3. Endemic species belonging to the Far Eastern zone of endemism (EA).
4. Southern tropical (ST).

In addition to these four complexes, there is also a single artificial group of widely distributed non-revised taxa (WS).

These findings suggest that this region is a mixing zone of the fauna of boreal and tropical origins. This mixing can be observed by analyzing both the species lists for separate sub-regions and the composition of the species “communities” (taxocoenoses) in each water body along a c.a. 2200-km north–south transect from the Khabarovsk area in Russia to Jeju Island, located south of the Korean Peninsula [36].

These data were re-enforced by phylogenetic and phylogeographic studies of several cladoceran species groups [45–52]. A few important conclusions were made, first of all, concerning the timing of the species dispersion. It was found that some usual cladoceran taxa and phyloclades in the Far East were differentiated in the Beringian zone in the Pleistocene and colonized more southern territories during the Late Pleistocene or the Early Holocene [45,53–55]. A pre-Pleistocene relict origin was directly shown for several local endemic taxa [55–57]. Therefore, it was concluded that the faunistic complexes are different not only in terms of their region of origin, but also in the timing of their differentiation. Previously, Korovchinsky [58] proposed that the subtropics and neighboring territories are regions with high numbers of surviving relicts in the course of the continuous mass extinctions from the Oligocene to the Pleistocene. A similarly high concentration of pre-Pleistocene relict lineages is characteristic of the cladocerans of the Mediterranean region [59–61].

The aforementioned phylogeographic studies confirmed the relict status of the endemic Far Eastern cladocerans. These old relicts (endemic to the region, EA) had a significant advantage compared to other faunistic complexes in the colonizing of new water bodies due to the strong climate de-aridification in the Late Pleistocene/Holocene [62,63]. As a result, they monopolized at least some of the habitats in the water bodies of this region, preventing the dispersion of boreal taxa towards the south and tropical taxa towards the north [63]. Therefore, the congruence (whether it is full or partial remains unknown) of the zone of endemism and the transitional zone between the boreal and tropical fauna may be explained based on priority effects. However, it is worth noting that the timing of the differentiation and dispersion of tropical taxa remains poorly understood.

During the last decade, it was shown that the species composition of faunistic complexes of the Cladocera undergoes seasonal changes—even in the same water body [62]. In addition, we found that, in different lakes, similar functional associations (planktonic, phytal, and benthic) are represented by different taxa, and that the portion of endemics is significantly higher among the taxa involved in these associations. This pattern may reflect colonization history, whereby the old endemics have an advantage, leading to the monopolization of the lakes before the appearance of younger boreal and tropical taxa [63].

However, to date, nothing is known about the possible differences in the proportion of endemic/boreal/tropical taxa in water bodies of different types (i.e., permanent and temporary) and among the plankton and littoral biotopes within this zone. We hypothesized that such differences are significant and that they may reflect the history of colonization by different faunistic complexes.

2. Materials and Methods

The dataset of identifications used here (Supplementary Table S1) is similar to that used by Garibian et al. [36], but it was significantly updated, i.e., some samples were added. In contrast, all samples from Zeya River basin by Garibian et al. [36] were removed from our analysis as we tried to study a latitudinal transect with a minimal contribution of a longitudinal factor (i.e., the distance from the Pacific Coast with the strongest summer influence of the Monsoon). Note that even in a previous study it was shown that latitude alone, not longitude, is the main factor shaping the species composition in the region [36]. Furthermore, substantial seasonal differences in the cladoceran species abundance and association composition [62] forced us to use the samples collected at summer months only. As a result, we included in our analysis 422 qualitative samples from 343 water bodies taken in 2002–2021, from late June to earlier September. Note that a single total sample was taken from each small water body, and few total samples were taken from pelagic and littoral zones of each large water body. In each case, several hundred liters of water were filtered. In the laboratory, each sample was examined totally with aim of forming a species list for each locality. Some specimens in these samples were re-identified based on new data obtained after the revisions of some genera [18]. Newly collected samples were analyzed following the protocol described in our previous publications [36,62]. All specimens identified up to the genus level (juveniles, ephippia of the Anomopoda, deformed specimens, separate body parts) were excluded from our analysis.

All water bodies were grouped into sub-regions by their geographical coordinates using non-hierarchical K-means clustering method [64]. The cluster assignments were initially random; items were then moved in an iterative procedure to the cluster which had the closest cluster mean, and the cluster means were updated accordingly. The result of the clustering depended to some extent upon the initial, random ordering, and cluster assignments may therefore have differed from run to run. Therefore, 100 runs with changing random seeds and numbers of initial clusters were performed, and maximum variance explained (98.72%) with minimum within-cluster sum of squares (WGSS 255.5) was achieved. Two additional conditions were taken into account. On one hand, Jeju Island is initially declared as an independent sub-region due to its geographic isolation and the confirmed specificity of its fauna [62]. On the other hand, a preliminary study of the relationship between the number of species and sampling effort demonstrated a strong influence of the sample number and the specimen number, which was consistent with the modern concept of species diversity [65,66]. Note that six clusters used here (representing 261 water bodies outside Jeju Island) were also mostly equal in terms of the number of water bodies included. As a result, we analyzed seven sub-regions (see Figure 1a). This regionalization was different from that conducted by Garibian et al. [36].

Characteristics of resulting sub-regional division and its correlation with freshwater ecoregions according to Abell et al. [67] realized on the WWF/TNC website [68] are summarized in Table 1.

Each water body was assigned to either temporary or permanent group, based on a description made by a sample collector or on the satellite image of studied area by Yandex Satellite Map (www.yandex.ru, accessed on 1 December 2022). Both methods make it possible to find obvious signs of complete drying in some phases of the water-body seasonal cycle. Roadside ditches, drying oxbows, rice fields, all puddles, and tanks were also automatically assigned to temporary water bodies. Otherwise, all other water bodies were assigned to the permanent group. The number of water bodies and the number of records belonging to each water body type were calculated for each sub-region. All

revealed species were subdivided into planktonic (PL) and benthic + phytophilous (BP), according to data from Korovchinsky et al. [18], and the number of records belonging to each biotope was calculated for each sub-region.

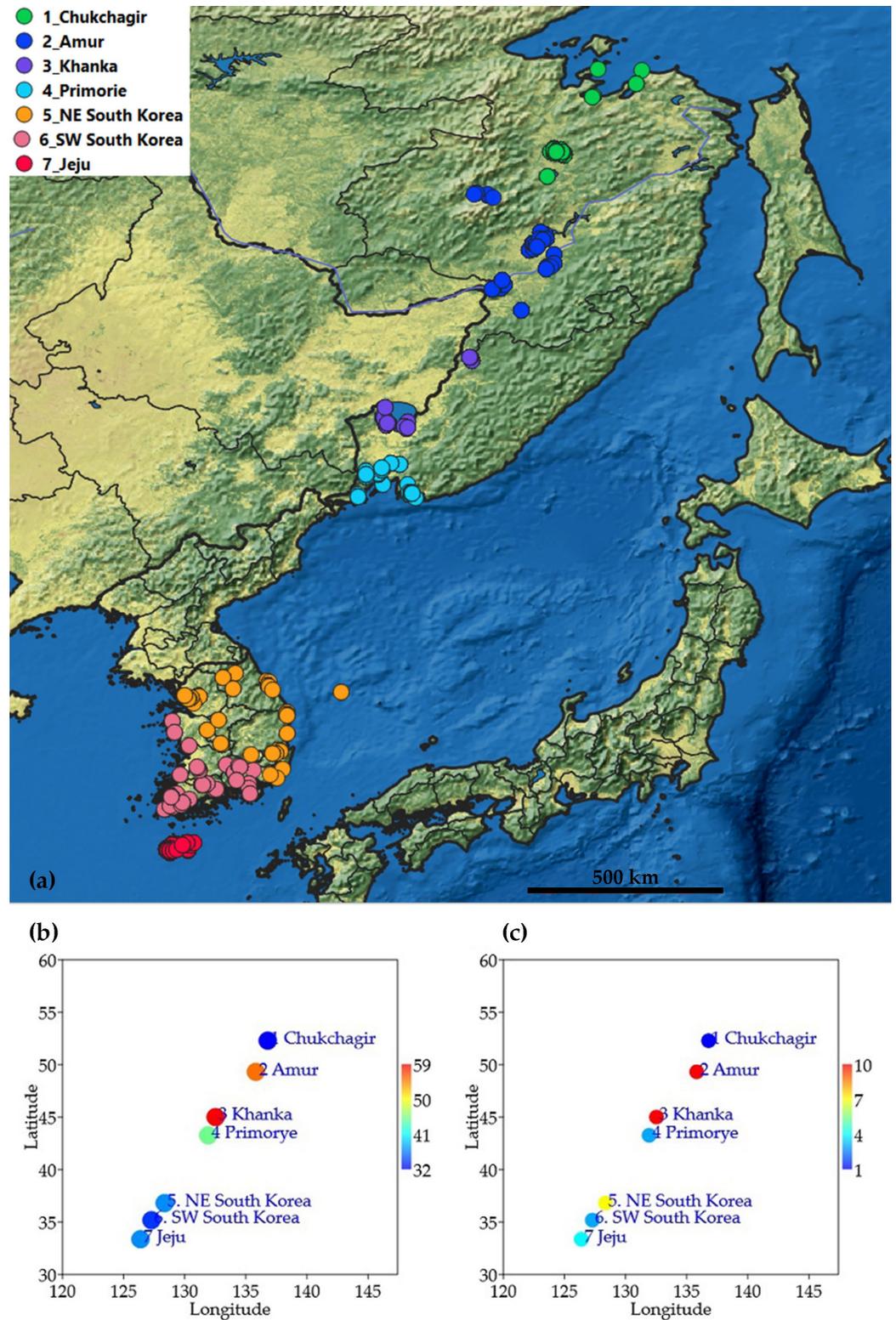


Figure 1. Region of study with sampling localities and sub-regions used in our analysis (a), total number of species in each sub-region (b), and total number of endemic species in each sub-region (c). Color temperature codes the number of species in each sub-region.

Table 1. Sub-regions used in this study with the number of water bodies, number of identifications, and information on their belonging to particular freshwater ecoregions [68].

Sub-Region	Water Bodies Total	Permanent	Temporary	Number of Identifications	Freshwater Ecoregion	Mean Latitude, °N	Mean Longitude, °E
1. Chukchagir	34	33	1	197	615, 616	52.29	136.79
2. Amur	44	31	13	276	616	49.32	135.82
3. Khanka	49	41	8	273	616	45.01	132.53
4. Primorye	43	17	26	161	641	43.27	131.93
5. NE South Korea	40	35	5	151	638, 639	36.81	128.36
6. SW South Korea	51	35	16	185	638, 639	35.18	127.28
7. Jeju	82	63	19	419	639	33.36	126.38

An empirical randomized species-accumulation curve depending on the sampling effort (the number of samples analyzed) was constructed in the EstimateS 9.1 package [69], with five different non-parametric species estimators, Chao1, Chao2, Jackknife1, Jackknife2, and Bootstrap, for the species from temporary vs. permanent water bodies, and for planktonic vs. benthic + phytophilous species. We chose the best (among five) model according to the minimum dispersion of predicted values for each step.

In order to estimate how the species belonging to different biotopes were distributed over temporary and permanent water bodies, we excluded 81 samples with a single species record. Note that these samples (mostly containing a single PL species) and their species distribution differed significantly from the rest of dataset: Kolmogorov–Smirnov paired-samples test [70] for equal distributions $D = 0.54803$, permutation p (999 Monte Carlo permutation) = 0.001, Anderson–Darling test [71] for equal distributions $Z = 21.819$, permutation p (999 Monte Carlo permutation) = 0.001.

Non-parametric Mann–Whitney test [72] was used to check the differences in average number of PL and BP species per water body in two groups of water bodies in all studied sub-regions; average number of PL and BP taxa per water body in each sub-region was visualized.

Next, all taxa were assigned to four geographic faunistic complexes (WE, EAA, EA, ST, see above) and an artificial group of non-revised widely distributed species (WS) according to Kotov [35], updated according to Kotov et al. [62] and Chertoprud et al. [63] (Table 2).

The graphs visualizing number of species belonging to each faunistic complex in each sub-region, ST and WE in all biotopes, ST and WE in PL and BP, ST and WE in PL only, and ST and WE in BP only are drawn.

Linear regression model (OLS method; the permutation test on correlation (r^2) used 9999 replicates) was applied to reveal the relation between the number of endemic taxa and a general number of the taxa revealed in a certain sub-region. Finally, the graph visualizing the portion of endemic taxa in total dataset, in permanent and temporary water bodies, portion of endemic taxa among PL species, BP species, and PL and BP species simultaneously was created, and then the same was performed with the portion of endemic taxon records.

All calculations and visualization of the graphs were performed in the STATISTICA 12 statistical analysis package and PAST 4.11 package [73].

Table 2. Species found in each sub-region and their placement in planktonic or benthic + phytophilous group and geographic faunistic complex (see abbreviations in the text).

Taxon	1. Chukchagir	2. Amur	3. Khanka	4. Primorye	5. NE South Korea	6. SW South Korea	7. Jeju	Biotope	Faunistic Complex
<i>Acroperus angustatus</i>	+	+	+	+				BP	WE
<i>A. harpae</i>	+	+	+	+				BP	WE
<i>Alona guttata</i>	+		+	+	+	+	+	BP	WS
<i>A. quadrangularis</i>				+		+		BP	WE
<i>Alonella excisa</i>	+	+	+	+	+	+	+	BP	WS
<i>Anchistropus emarginatus</i>			+					BP	WE
<i>Biapertura affinis</i>	+	+	+	+	+	+		BP	WS
<i>B. sibirica</i>	+	+		+				BP	WE
<i>Bosmina fatalis</i>		+	+		+			PL	EA
<i>B. longirostris</i>	+	+	+	+	+	+	+	PL	WS
<i>Bosminopsis zernowi</i>		+	+	+	+	+		PL	WE
<i>Bunops serricaudata</i>			+	+				BP	WE
<i>Camptocercus fennicus</i>	+							BP	WE
<i>C. smirnovi</i>	+	+						BP	EEA
<i>C. uncinatus</i>	+	+	+	+	+	+	+	BP	EEA
<i>C. vietnamensis</i>					+			BP	ST
<i>Ceriodaphnia cornuta</i>					+	+	+	PL	ST
<i>C. laticaudata</i>			+	+				PL	WS
<i>C. megops</i>					+			PL	WS
<i>C. pulchella</i>	+	+	+	+				PL	WS
<i>C. quadrangula</i>	+				+		+	PL	WS
<i>C. reticulata</i>		+	+				+	PL	WS
<i>C. rotunda</i>			+					PL	WS
<i>Chydorus cf. sphaericus</i>	+	+	+	+	+	+	+	BP	EEA
<i>Coronatella jejuana</i>							+	BP	EA
<i>C. rectangula</i>	+	+	+	+	+	+	+	BP	WS
<i>C. trachystriata</i>		+			+			BP	EA
<i>Daphnia cristata</i>		+	+					PL	WE
<i>D. curvirostris</i>	+	+	+	+				PL	WE
<i>D. galeata</i>		+	+	+	+	+	+	PL	WE
<i>D. jejuana</i>							+	PL	EA
<i>D. koreana</i>					+			PL	EA
<i>D. korovchinskyi</i>		+						PL	EA
<i>D. longispina</i>				+				PL	WS

Table 2. Cont.

Taxon	1. Chukchagir	2. Amur	3. Khanka	4. Primorye	5. NE South Korea	6. SW South Korea	7. Jeju	Biotope	Faunistic Complex
<i>D. obtusa</i>							+	PL	WS
<i>D. pulex</i>			+					PL	WS
<i>D. sinensis</i>		+	+	+	+	+	+	PL	WE
<i>D. sinevi</i>		+	+	+				PL	EA
<i>Diaphanosoma amurensis</i>		+	+				+	PL	EA
<i>D. brachyurum</i>		+					+	PL	WE
<i>D. chankensis</i>			+					PL	EA
<i>D. dubium</i>	+	+	+	+	+	+	+	PL	EA
<i>D. macrophthalma</i>		+	+	+	+	+		PL	EA
<i>D. pseudodubium</i>		+						PL	EA
<i>D. sarsi</i>							+	PL	ST
<i>D. transamurensis</i>			+		+			PL	EA
<i>Disparalona chappuisi</i>		+	+	+	+	+		BP	ST
<i>D. ikarus</i>	+	+	+	+	+	+	+	BP	ST
<i>D. rostrata</i>			+					BP	WE
<i>Drepanothrix dentata</i>	+							BP	WE
<i>Dunhevedia crassa</i>					+		+	BP	ST
<i>Eurycercus macracanthus</i>	+	+	+	+				BP	EEA
<i>Flavalona costata</i>	+	+	+	+	+	+	+	BP	WS
<i>F. rustica</i>			+					BP	WS
<i>Graptoleberis testudinaria</i>	+	+	+	+				BP	WS
<i>Illyocryptus acutifrons</i>	+							BP	WE
<i>I. cuneatus</i>			+		+			BP	WE
<i>I. raridentatus</i>				+		+	+	BP	ST
<i>I. spinifer</i>		+	+		+	+	+	BP	ST
<i>I. yooni</i>	+		+	+	+			BP	ST
<i>Kurzia latissima</i>		+	+	+				BP	WE
<i>K. longirostris</i>						+		BP	ST
<i>Leberis diaphanus</i>							+	BP	ST
<i>Leptodora kindtii</i>		+	+					PL	WE
<i>L. richardi</i>			+					PL	EA
<i>Leydigia acanthocercoides</i>						+		BP	WE
<i>L. ciliata</i>							+	BP	ST
<i>L. lousi</i>					+			BP	ST
<i>Limnosida frontosa</i>	+							BP	WE
<i>Macrothrix laticornis</i>				+				BP	WE

Table 2. Cont.

Taxon	1. Chukchagir	2. Amur	3. Khanka	4. Primorye	5. NE South Korea	6. SW South Korea	7. Jeju	Biotope	Faunistic Complex
<i>M. rosea</i>		+	+	+	+		+	BP	WE
<i>M. triserialis</i>					+		+	BP	ST
<i>M. vietnamensis</i>						+	+	BP	ST
<i>Megafenestra aurita</i>				+				PL	WE
<i>Moina affinis</i>					+			PL	WS
<i>M. lipini</i>		+		+				PL	WE
<i>M. macrocopa</i>		+		+	+		+	PL	WE
<i>M. micrura</i>		+	+	+		+	+	PL	WS
<i>M. weismanni</i>			+		+	+		PL	EA
<i>Monospilus daedalus</i>		+						BP	EA
<i>Nedorchynchotalona chiangi</i>		+	+					BP	EA
<i>Picripleuroxus denticulatus</i>						+		BP	ST
<i>P. laevis</i>		+	+			+		BP	WE
<i>P. quasidenticulatus</i>		+	+		+	+	+	BP	ST
<i>P. striatus</i>		+	+					BP	WE
<i>Pleuroxus aduncus</i>		+	+			+		BP	WS
<i>P. truncatus</i>	+	+						BP	WE
<i>Polyphemus pediculus</i>	+	+	+					PL	WS
<i>Pseudochydorus globosus</i>		+	+	+		+		BP	WE
<i>Pseudosida szalayii</i>						+	+	BP	ST
<i>Scapholeberis mucronata</i>	+	+	+	+				PL	WS
<i>S. smirnovi</i>		+	+	+	+	+	+	PL	ST
<i>Sida crystallina</i>	+	+		+		+		BP	WE
<i>S. ortiva</i>		+	+	+	+	+	+	BP	EEA
<i>Simocephalus congener</i>			+					BP	WS
<i>S. exspinosus</i>		+	+	+				BP	WS
<i>S. mixtus</i>	+	+	+	+	+	+	+	BP	WS
<i>S. serrulatus</i>	+	+	+	+			+	BP	WS
<i>S. vetuloides</i>	+							BP	EEA
<i>S. vetulus</i>		+	+	+			+	BP	WS
<i>Streblocerus serricaudatus</i>	+							BP	WE
Total	32	55	59	45	37	34	37	101	101

3. Results

Out of 422 samples, 1662 records of the cladocerans were identified up to the species level; 101 species were revealed.

The permanent and temporary water bodies displayed different levels of species diversity: 99 species were found in the former, and 52 species were found in the latter. The species-accumulation curves for the temporary vs. permanent water bodies are represented in Figure 2a. The estimated species numbers for the temporary (59.3) and permanent (110.6) groups were best assessed by Bootstrap method; the values were sufficiently close to the observed species numbers for the whole dataset for the species diversity in the two water-body groups to be considered well-studied.

The biotopes also varied in the species abundance; 61 species belonged to BP and 40 species belonged to PL (planktonic) groups. Figure 2b presents the species-accumulation curves for the BP and PL for the samples in which BP or PL species were present (276 and 265, respectively; most of the samples contained BP and PL species simultaneously). The estimated species numbers for the benthic-phytoplanktonic (BP = 67.5) and planktonic (PL = 43.9) groups were also best assessed by the Bootstrap method the values were sufficiently close to the empirical numbers for the whole dataset for the biotope species diversity to be considered well-studied.

The regional distribution of the species and species records by biotope is represented in Table 3. Note that there was no obvious correlation between of the particular sub-regions to which the water bodies belonged and the total species number (Figure 1b).

Table 3. Number of records/number of species by biotope in each sub-region.

Sub-Region	BP	PL	Total
1. Chukchagir	147/25	50/7	197/32
2. Amur	193/32	83/23	276/55
3. Khanka	158/34	115/25	273/59
4. Primorye	89/28	72/27	161/45
5. NE South Korea	100/21	51/16	151/37
6. SW South Korea	109/24	76/10	185/34
7. Jeju	283/22	136/15	419/37
Total	1079/61	583/40	1662/101

The final number of water bodies analyzed and the average numbers of PL and BP taxa they contained are represented in Table 4.

Table 4. Mean number of BP and PL species in the water bodies of different types.

	Water Bodies	BP Species ($n \pm SD$)	PL Species ($n \pm SD$)	EA ($n \pm SD$)
Permanent	218	4.17 \pm 3.48	2.06 \pm 1.67	0.41 \pm 0.77
Temporary	60	2.18 \pm 2.42	1.77 \pm 1.09	0.30 \pm 0.57
Total	278	3.74 \pm 3.37	2.00 \pm 1.56	0.38 \pm 0.72

The non-parametric Mann–Whitney test on the two groups of water bodies showed that the average number of PL species per water body did not differ in permanent and temporary waters, but the number of BP species was significantly lower in the temporary water bodies compared to the permanent waters (at $p < 0.05$) (Table 5). The average numbers of PL and BP taxa in each studied sub-region are represented in Figure 3. It can be concluded that the numbers of PL and BP taxa were comparable in the temporary water bodies, while in the permanent water bodies, the number of BP species was always higher than the number of PL species.

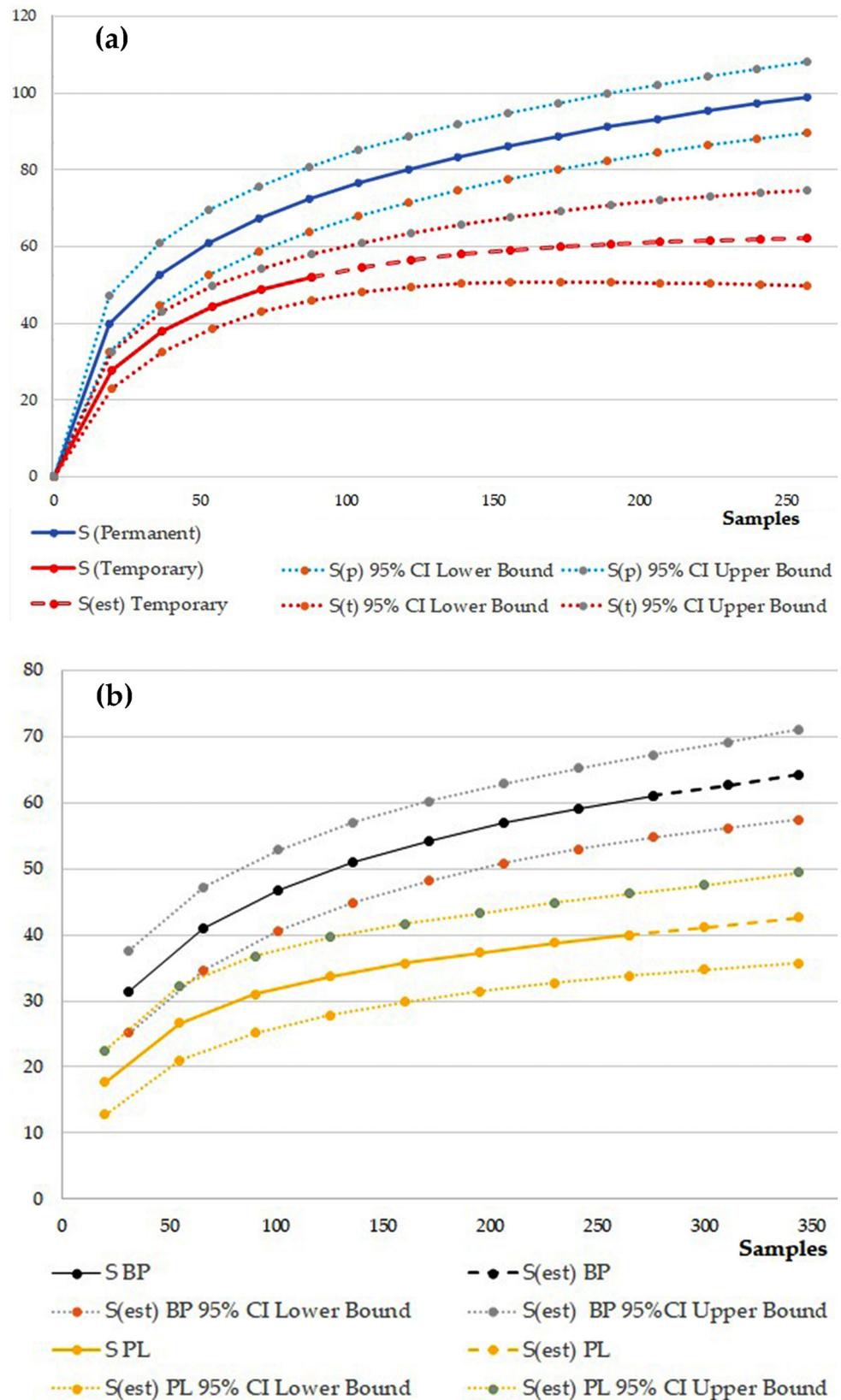


Figure 2. Species-accumulation curve for temporary and permanent water bodies (a) for planktonic and benthic + phytophilous taxa (b) in whole region.

Table 5. Results of the non-parametric Mann–Whitney test of differences between PL and BP species in permanent and temporary waters.

	Rank Sum Permanent	Rank Sum Temporary	U	Z	p-Value	Z Adjusted	p-Value	Valid N Permanent	Valid N Temporary
PL species	30,701.50	8079.50	6249.50	0.52678	0.59834	0.54154	0.58813	218	60
BP species	32,886.00	5895.00	4065.00	4.48807	0.00007	4.51964	0.00006	218	60

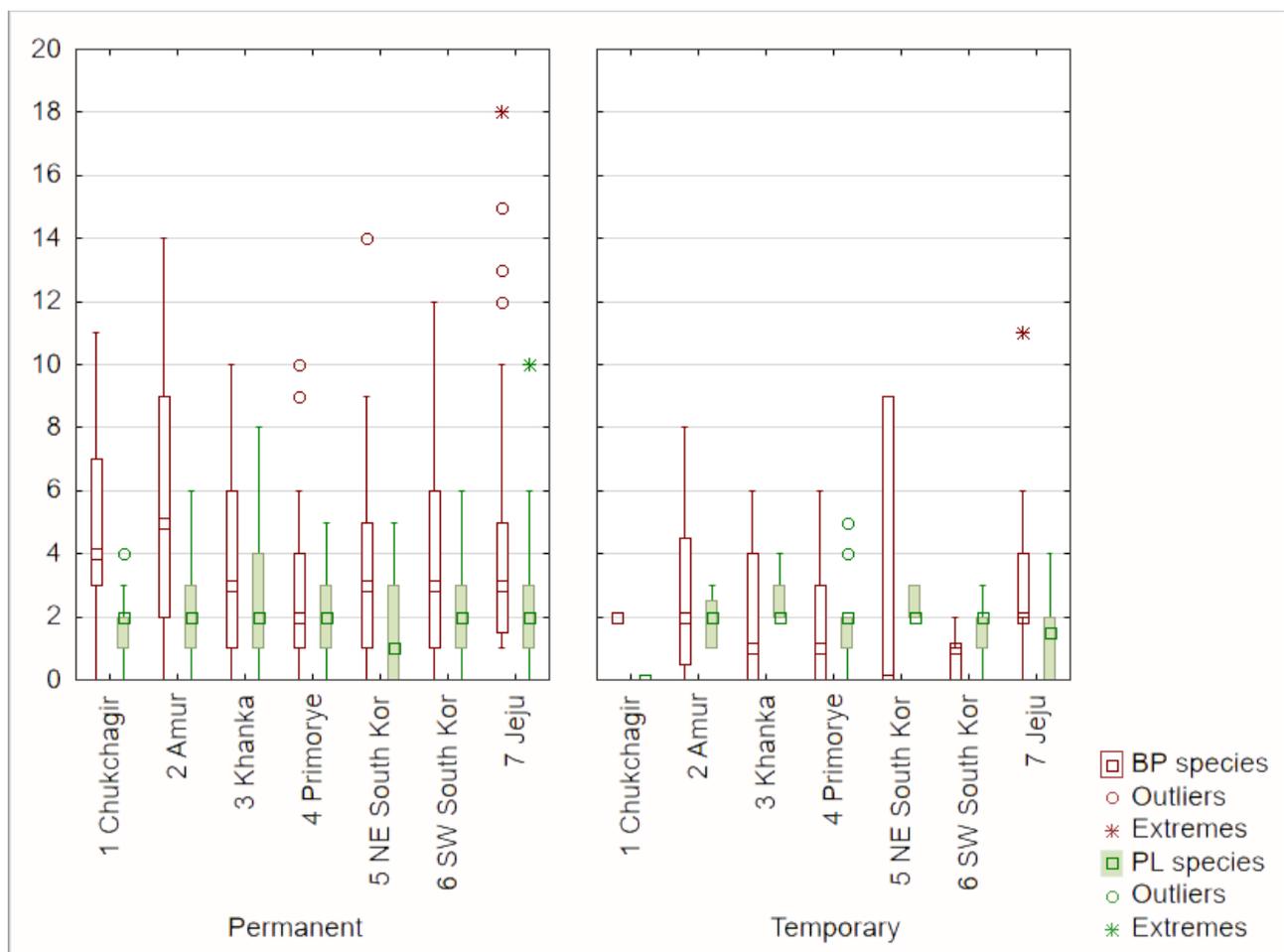


Figure 3. Average number of PL and BP species in a water body from each sub-region.

The general composition of the regional fauna coincided with previously published data [15,36,62]—the WE were gradually displaced by the ST species as the latitude dropped (Figures 4 and 5a). At the same time, endemic taxa were present in all the zones, and there was no obvious correlation between the particular sub-region to which the water bodies belonged and the number of endemic species (Figure 1c).

However, when we analyzed two types of water bodies, and the PL vs. BP taxa separately, a more complicated pattern was revealed (Figure 5b). The proportion of species belonging to the WE in the PL clearly decreased towards the south, but it never exceeded the proportion of ST species, and *vice versa* (Figure 5c). In contrast, all the sub-regions could be subdivided, according to the proportion of WE and ST, into two zones based on the BP taxa: with a prevalence of WE in the north, and with the prevalence of ST in the south, with a sharp change at Primorye—NE–South Korea interval (North Korea was not represented by samples).

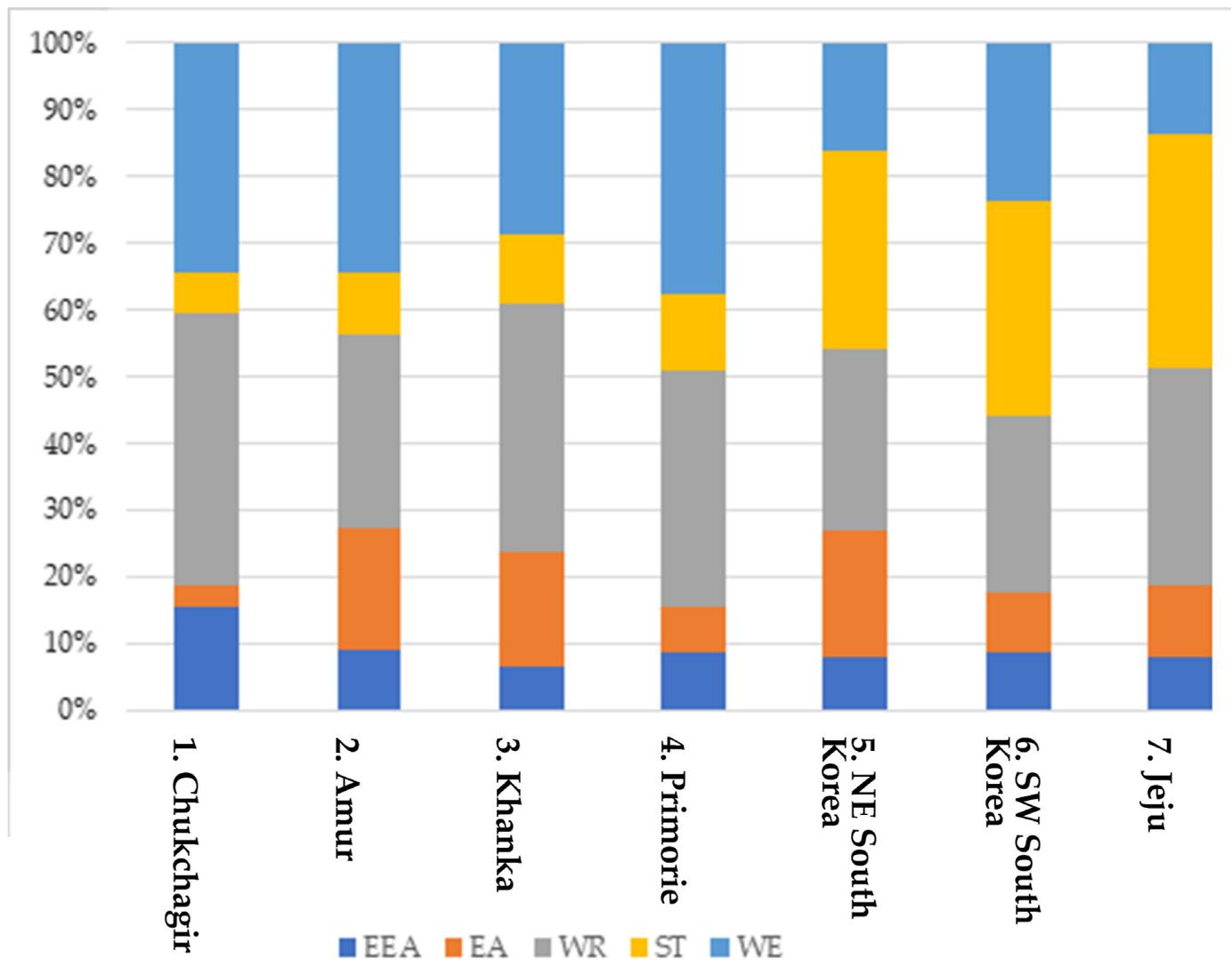


Figure 4. Proportions of the species belonging to different faunistic complexes in different sub-regions.

The average number of endemic taxa per water body was not different for the PL and BP taxa (Table 4, $p = 0.91$). A portion of the local endemic species (EA) was comparable in different sub-regions, and there was no latitudinal tendency in its change. Moreover, in reality, fluctuations in the numbers of taxa found in the different sub-regions can be directly explained by the somewhat different sampling efforts, because there was a significant correlation between the number of endemic taxa found and the total number of species found ($r = 0.84$, $r^2 = 0.70$, $t = 3.4692$, permutation $p = 0.0196$), as represented in Figure 6a. The best predictor available was the number of the PL group taxa revealed in a certain sub-region (Figure 6b). This approximation was described effectively by the linear regression model with the ordinary least-squares algorithm ($r = 0.91$, $r^2 = 0.82$, $t = 4.9123$, permutation $p = 0.0056$). However, the endemic species were not equally distributed among the permanent and temporary waters (Figure 6c). Finally, the records of EA species were mainly PL: PL; only endemic species were found in eighty-seven samples, five samples had endemic BP species only, and a single sample had PL (*Moina weismanni*) and BP (*Coronatella trachystriata*) endemic species simultaneously (Figure 6c).

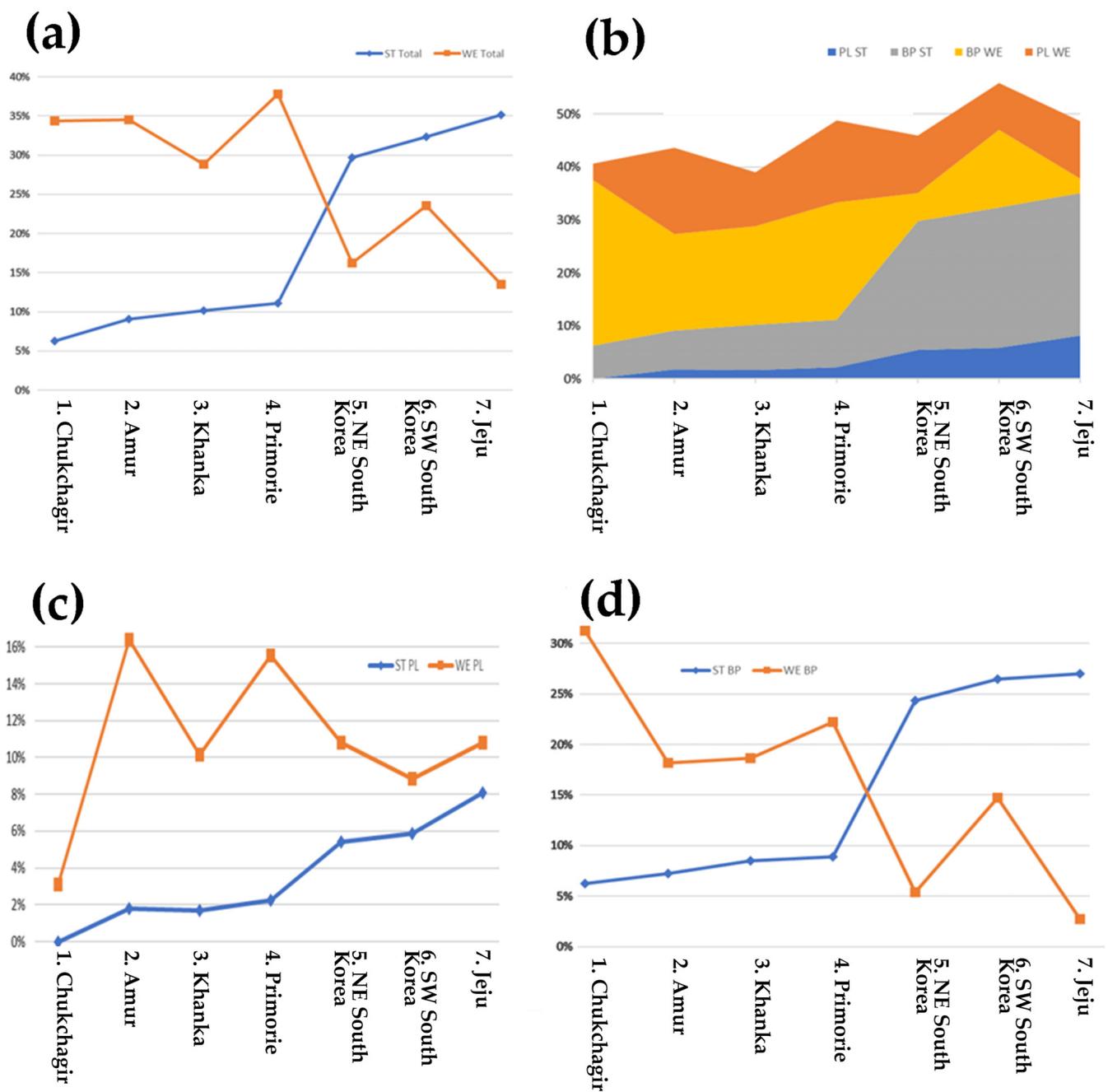


Figure 5. Change in proportion between the numbers of species belonging to different geographic faunistic complexes in the region, from most northern (1. Chukchagir) to most southern (7. Jeju) sub-region: (a) ST and WE in all biotopes; (b) ST and WE in PL and BF area charts; (c) ST and WE in PL only; (d) ST and WE in BP only.

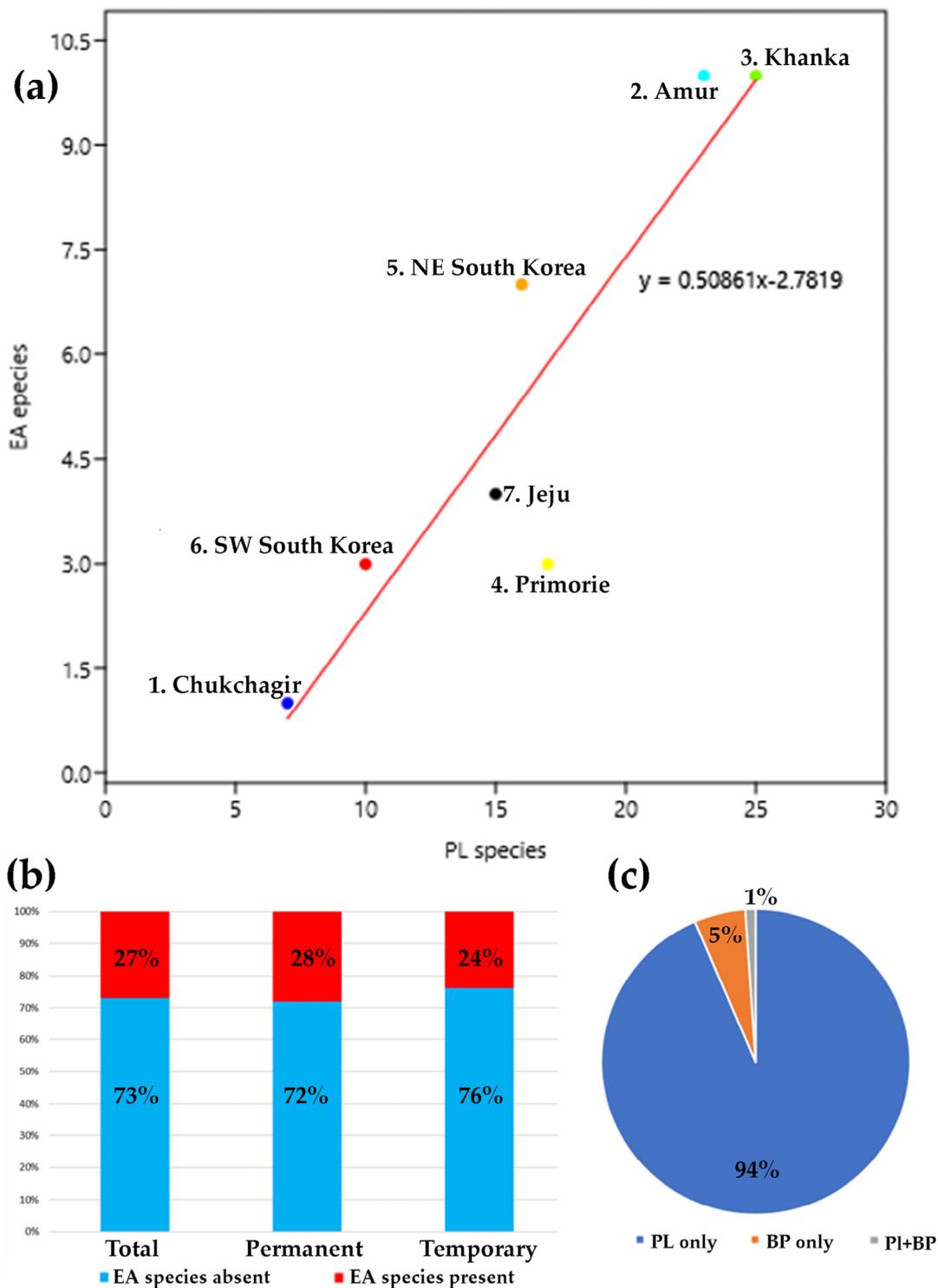


Figure 6. Linear regression model (OLS method) of EA species distribution between sub-regions in current dataset with total number of species. Best approximation is model with number of PL species (a). Portion of endemic taxa in total dataset, in permanent and temporary water bodies (b). Portion of water bodies, where determinations of endemic taxa are PL species only, BP species, and PL and BP species simultaneously (c).

4. Discussion

Endemics are typically concentrated in areas where climate change is weakest [74], and our region is no exception, having served as a refugium for cladocerans during the

Pleistocene [45]. Initially, we expected that the proportion of endemic taxa would be higher in temporary waters, which frequently serve as refugial habitats for relicts [75–77]. Moreover, in some regions, their species composition has remained unchanged for the last million years [78]; this has been directly demonstrated for cladocerans and large branchiopods [79]. However, in our study region, the rates of EA records in the permanent and temporary waters were not significantly different (Table 4). The proportion of temporary water bodies containing relict taxa was slightly lower than the number of permanent water bodies containing relicts (Figure 6c). We also observed another pattern: the proportion of both EA taxa and their records was much higher among planktonic taxa than among littoral and benthic taxa.

It is well-known that the number of species in littoral zones is higher than in plankton [80]. In the Fat East, planktonic species are relatively numerous, and we may hypothesize that it can be explained by the great number of water-body types in this region. The pattern observed in this study, according to which the level of endemism was higher among the planktonic species than among the littoral and benthic species, is noteworthy. This phenomenon was observed in some animal groups, while other researchers have shown controversial results. For instance, in the Caspian “Sea”, which is a large, salty lake, there are many endemic planktonic cladocerans belonging to the Order Onychopoda [81,82]. Several onychopod genera have rapidly expanded their distribution ranges and become dangerous invasive species in recent years [83,84]. Generally, most invasive cladoceran species are plankton [85]. According to Cristescu and Hebert [86], the Pontic–Caspian basin was presumably the center of their differentiation from the Miocene to the Pleistocene, although recent molecular clock calculations suggest that their differentiation may be even older, dating back to the Mesozoic [87]. Cristescu et al. [88] compared the differentiation of benthic (amphipods) and planktonic (cladocerans) taxa in the region and noted that “based on standard molecular clocks, the Black and Caspian lineages of benthic crustaceans diverged at varied intervals from 1 to 8 million years ago. By contrast, planktonic lineages are more recent with their divergence occurring in the last million years.” However, it should be noted that distant taxa of plankton and benthos were compared in this study.

A fully contrasting pattern was observed in Lake Baikal, where all the endemics among the Cladocera are benthic, and plankton is represented by the common “Siberian” taxa [89,90]. However, the strong depth differentiation of the Baikalian fauna is well-known [91,92]. It has been shown that the age of the fauna, including the Baikalian endemics, is different [93]. In seas, the rate of endemics in the benthos is usually higher than in planktonic taxa, as the latter are more vagile. Furthermore, many planktonic species are cosmopolitan or have a very wide distribution range [94]. However, this situation is far removed from that in continental water bodies, as the latter fauna are subdivided into discrete water bodies, with limited interchange between them, even for plankton capable of long-distance passive dispersal.

It should be noted that the number of endemic species is correlated with the total species richness within a macro-taxon [94,95], which primarily reflects the degree of exploration of the taxon. Unfortunately, there is a general tendency in micro-crustacean studies to focus strongly on pelagic plankton in large lakes [96,97], with less attention paid to the littoral zones and the bottoms of large water bodies (which contain significantly higher numbers of species than the pelagic zones), as well as the fauna in small temporary waters.

The observed differences between planktonic and littoral, and between large and small water bodies may be partially explained by a better understanding of planktonic species, particularly in terms of species identification. Some may argue that the higher rate of endemic taxa among planktonic species reflects the fact that they have been studied in greater depth, and that further revisions could reveal more endemic taxa among littoral forms rather than planktonic forms. However, in our analysis, the numbers of non-revised planktonic and littoral taxa were exactly the same. Moreover, there is direct genetic evidence that many WS taxa, including *Bosmina* cf. *longirostris*, *Daphnia* cf. *longispina*, *D.* cf. *obtusa* and *D.* cf. *pulex*, *Moina* cf. *micrura*, *Polyphemus* cf. *pediculus*, and *Scapholeberis* cf. *mu-*

cronata, represent assemblages of cryptic species, even in the Far East [44–46,48,50,56,98,99]. Therefore, we believe that further revisions will not alter the pattern observed in our study. In other words, our original conclusion is not an artifact of a biased taxonomic study.

The varying rates of relicts among Far Eastern planktonic species could reflect differences in the evolutionary history of different cladoceran families and genera. However, further research is needed to explore this question.

Our conclusion regarding the differences between plankton and benthos/littoral in the proportion of relicts has a direct impact on the analysis of latitudinal faunal changes. The strong difference in the pattern of boreal/tropic faunal change (from Western Eurasia to Southeast Asia) between plankton and benthos/littoral could be directly related to the different proportions of faunal complexes in the plankton, primarily the significant proportion of EA taxa and their records. We previously proposed the hypothesis that the strong representation of EA taxa in Late Pleistocene–Early Holocene water bodies may have prevented the penetration of further colonists from the north and south. The proportion of relict taxa is low in the benthos/littoral, and we observed a sharp change in dominance across our transect, with WE dominating in the northern sub-regions (1–4) and ST dominating in the southern sub-regions (5–7), with an interval (4–5) in which the boreal taxa were substituted by tropical taxa. We can assume that this sharp pattern appeared because almost nothing prevented their dispersion in the latitudinal direction until the boundary where they met during their arrival. In contrast, the rates of WE and ST taxa never exceeded 16% in any of the studied sub-regions, and the rate of WE fell from 16% to 10%, while the rate of ST grew from 0% to 10% from region 1 to region 7. We suggest that the lower rates and the non-mixing of fauna can be explained by the strong rate (sometimes dominance) of the relicts that colonized these water bodies before the arrival of SE from the north and ST from the south.

We agree that “climatic heterogeneity, orographic barriers, past tectonic history, and the velocity of past climate change may play a major role in setting biogeographical boundaries” [6]. In the region of study, the climatic gradient is not overly strong, as all the sub-regions are located in the zone of the Asian Monsoon’s influence [100,101], and the climatic changes in this region were moderate compared to those in more northern regions due to the “buffering effect of the Pacific Ocean” [102]. The tectonic changes have been minimal in the studied transect since the Middle Pleistocene, with the exception of Jeju Island, with its particular fate [62]. In general, we can conclude that there are no clear geographic or climatic boundaries in the region of study.

5. Conclusions

However, “biogeographic patterns arise primarily through limits on dispersal” [103], and such limits can arise in a different, biotic manner. Although “few examples exist of large-scale patterns created by biotic interactions” [103], we believe that currently, the role of biotic interactions in the formation of biogeographic boundaries is significantly underestimated. Only a few authors have pointed to interspecific competition as a factor shaping species boundaries [104–106], including biogeographic boundaries [107–109]. Our hypothesis of the significant role of biotic interactions in the formation of biogeographic boundaries in Far Eastern Cladocera requires further testing. Moreover, we cannot state that we have revealed a universal pattern characteristic of other zones of freshwater endemism (such as the Mediterranean).

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d15060713/s1>. Figure S1: Change in proportion between the numbers of records belonging to different geographic faunistic complexes in the region, from most northern to most southern sub-region: (a) ST and WE in all biotopes; (b) ST and WE in PL and BF area charts; (c) ST and WE in PL only; (d) ST and WE in BP only. Table S1: Localities and species identified from each sample.

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