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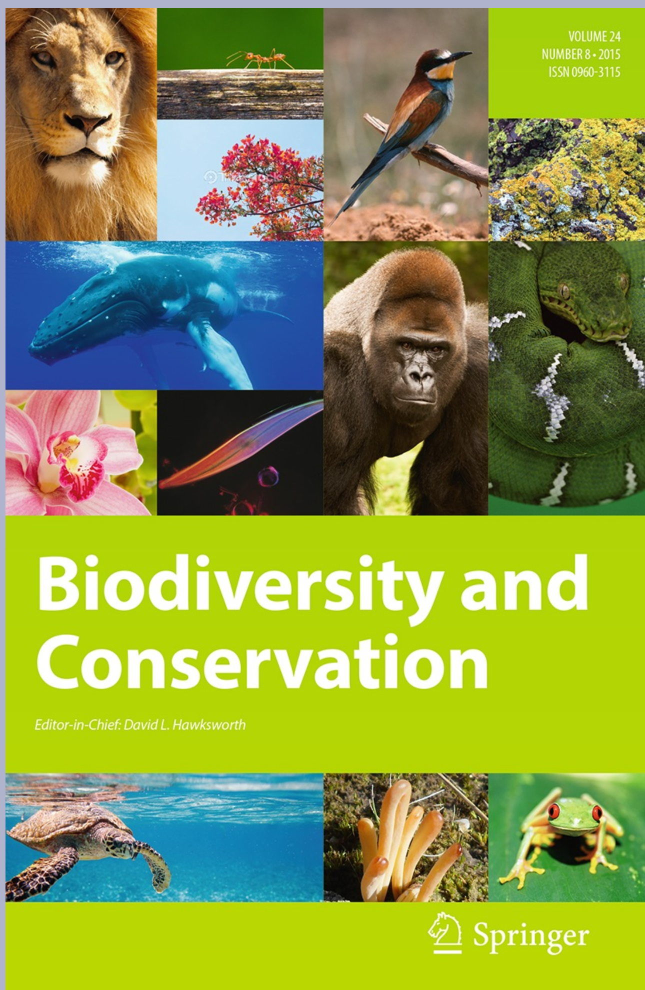

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ORIGINAL PAPER

How does the discrepancies among taxonomists affect macroecological patterns? A case study of freshwater snails of Western Siberia

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Abstract From the point of view of biogeographers and ecologists, taxonomy is not only a means of ordering life but also a source of some problems able to impede the progress in studies of large-scale patterns of biological diversity. Discrepancies among systematists caused, inter alia, by their different views on the species concept and criteria for species delineation, are commonly thought to provoke errors and misinterpretations in macroecological inferences. In this study, we discuss a case of freshwater gastropods of Western Siberia. Two systematic frameworks, developed in Western Europe and Russia and drastically different in number of accepted genera and species, were proposed to classify the Palearctic aquatic snails. Having compared two sets of diversity data generated on the basis of the two systematic frameworks, we found that their parameters do not differ significantly. Such patterns as latitudinal gradients in total species richness, portion of branchiate snail species, and portion of species of non-European origin proved to remain the same, irrespective of which taxonomic approach, Western European, or Russian, is accepted. The absence of reliable changes in macroecological patterns may be explained by nearly consistent "splitting effort" applied by the Russian taxonomists in their revision of different families of aquatic snails. Thus, though the European and the Russian

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systematic frameworks differ significantly in number of accepted species, the large-scale patterns of diversity based on the two approaches are qualitatively the same.

Keywords Freshwater snails · Diversity · Macroecology · Taxonomic uncertainty · Western Siberia

It is well recognized that many patterns revealed in current macroecological studies are critically dependent on quality of accumulated taxonomic work creating the systematic framework needed for analyses. In most cases, the species are used as data points in macroecological research (Jones et al. 2012), though, by contrast, in paleobiology, the genus rather than the species is used as a primary unit in quantitative analyses of mass extinctions, large-scale biogeographic or evolutionary changes or demonstration of adaptive radiations (Allmon 1992). There is a large body of case studies demonstrating the dependence of macroecological inferences on quality of taxonomic resolution (Sheppard 1998; Genner et al. 2004; Dillon and Fjeldså 2005; Mitchell and Meisterfeld 2005; Heger et al. 2009; Evangelista et al. 2014; Löbl and Leschen 2014). The so called *taxonomic bias* (Clark and May 2002; Nilsson-Örtmann and Nilsson 2010; Carrasco 2013) is thought to be among the most significant sources of errors and misinterpretations in macroecological studies able to distort their conclusions. Another factor that may potentially generate biased inferences is *taxonomic uncertainty* caused by, for example, different views of systematists on the nature of the biological species and criteria of taxa delineation (Hey et al. 2003; Isaac et al. 2004; Heger et al. 2009). The third source of problems that taxonomists unwittingly create for ecologists and biogeographers is *taxonomic inflation* (Isaac et al. 2004)—the presence in the lists of species a portion of taxa that are destined to become synonymized (Alroy 2002; Jones et al. 2012). A large deal of formally described species may be actually invalid that results in overestimation of biological diversity, though in some underexplored animal taxa the opposite situation, when accepted species represent, in reality, quite a number of unrecognized cryptic species, is also possible (Adamowicz and Purvis 2005; Stålstedt et al. 2013).

As a result, ecologists and biogeographers, being the "end users" of taxonomic information, are often hostile towards the endless debates among systematists (Mina et al. 2006), and they typically want something like a stable system of living organisms with "final and definitive" lists of taxa based on "objective" criteria for species and genera delineation (Dubois 1998; Bouchet 2006; Padial and de Riva 2006). The users are equally hostile to permanent changes in taxonomic names of plants and animals, though most of them are not aware that these changes are dictated by internationally adopted rules of nomenclature aimed to sustain the taxonomic stability rather than to promote a capricious reshuffling of names and museum labels. In response, some systematists proudly claim that "taxonomic stability is ignorance" (Dominguez and Wheeler 1997), and, thus, this discussion seems to be infinite.

Anyway, it has become almost a commonplace to think that discrepancies among taxonomists, including the textbook case of permanent war between "splitters" and "lumpers" (Jones et al. 2012), may seriously impede the progress in biogeographical and macroecological studies as well as create troubles for biological conservation (Isaac et al. 2004; Frankham et al. 2012). The most extreme proposals how to avoid it include, in particular, appeals to abandon altogether the species paradigm from the ecological and

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genetic studies as well as from conservation policy (Riddle and Hafner 1999; Hendry et al. 2000).

However, the situation may well be not so dark as it is sometimes assumed. For example, the results obtained by Jones et al. (2012) imply that the large-scale patterns of diversity and other macroecological conclusions may be qualitatively unaffected by taxonomic overdescription. Sangster (2009) has shown that the recent increase in bird species number may be explained by progress in taxonomical methodology rather than by increased "splitting effort". Thus, the form and strength of dependence of such patterns on the quality of taxonomic work need to be further studied by using data from a broader set of plant and animal taxa.

This paper represents a case study of spatial variation in diversity of aquatic snails (Mollusca: Gastropoda) of Western Siberia (Asiatic Russia). The general patterns of this variation were described and discussed by Vinarski et al. (2012a, b), but the existence of two drastically different taxonomic frameworks in current "freshwater" malacology makes this taxon a good model group for the study of how much the discrepancies among taxonomists may influence the relationships between parameters of diversity and geographical latitude.

In this study, we tried to estimate how much the discrepancies among taxonomists may influence the large-scale patterns of freshwater mollusk diversity. There are two reasons to select Western Siberian region as an area for such a study. First, its territory has been extensively explored by malacologists, and the data on distribution of most species of mollusks are available. Second, Western Siberia is a spacious plain where the main environmental gradients (temperature, humidity, seasonality and others) are very well pronounced, and a series of bioclimatic zones, from arctic deserts in north to dry steppes in south, is present within its boundaries. It makes Western Siberia a very suitable region to study large-scale patterns of diversity in continental mollusks and other animals.

Two systems of the Palearctic freshwater mollusca

Today, we lack a uniform and commonly accepted system of freshwater mollusks (both bivalves and gastropods) of Palearctic. Two disappointingly different systematic frameworks grounded on drastically different taxonomic philosophies have been developed in the last century. The first of them, called here "Western European", or, for short, simply "European", is a direct continuation of a long tradition of studies of freshwater mollusks by malacologists of Germany, England and France. Generally, the Western European malacologists prefer to accept "a characteristically small number of species, almost worldwide in distribution, but with a high degree of infraspecific interpopulation variation" (Russell-Hunter 1964, p. 102). Perhaps, the most perfect product of this approach is the list of continental mollusks of Europe compiled by a team of investigators working together under the Check List of European Continental Mollusca (CLECOM) initiative (Falkner et al. 2001). Though the CLECOM list was subjected to some criticism (Davis 2004), it is still serves as an authoritative source for taxonomic information and distributional data on freshwater snails and bivalves of Europe (except of its south and extreme eastern parts).

In the former USSR, a quite different approach to delimitation of species and genera of freshwater mollusks has been developed. It is designated here as the "Russian" one. The so called "Leningrad school" (Meier-Brook 1993), established by an influential Russian zoologist Yaroslav I. Starobogatov, introduced its own version of taxonomic framework

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for almost all families of Palearctic freshwater snails and bivalves. From the point of view of the Leningrad school, many of widely distributed and highly variable species accepted by European taxonomists, are, in reality, nothing but complexes of taxa of different ranks, from subspecies to species and even subgenera (Graf 2007). In practice, this persuasion has resulted in delimitation of a vast number of valid species, several times greater than Western European malacologists used to accept (Table 1). For example, a single species of viviparid snails, *Viviparus contectus* (Millet 1813), accepted by the European malacologists, is considered in Russia as a complex of as many as eight distinct species (Fig. 1).

The methodological basis of the taxonomic works carried out by Russian malacologists includes the biological species concept (BSC) as well as the so called "comparatorial method" invented by Logvinenko and Starobogatov (1971). In brief, this method is based on comparative study of subtle interspecific differences in shell coiling (in snails) or in curvature of the frontal contour of a shell valve (in bivalves) (see, for details, Shikov and Zatravkin 1991; Kafanov 1998; Graf 2007). Graf (2007) considers it as a separate species concept that is viewed by him as a reincarnation of the typological approach to species delineation opposed to BSC. It is not wholly correct since Starobogatov itself was a supporter of BSC and several times discussed its application to systematization of freshwater mollusks (Starobogatov 1968, 1996). However, it is the fact that using the comparatorial method has led to drastic increase in number of species accepted by Russian malacologists. In most cases, the existence of reproductive isolation between "comparatorial" species (required by BSC) was deduced indirectly from observed statistical differences between the samples of alleged species (Starobogatov 1996).

Discussion of the advantages and shortages of both taxonomic approaches was beyond the scope of our research. Here, we accept the two systems as equally suitable systematic frameworks dealing with approximately the same set of taxa. Since the determination key compiled by Starobogatov et al. (2004) on the basis of results of the Leningrad School taxonomy is still in wide use in Russia and some other ex-USSR countries, the problem of possible influence of taxonomic debates on ecological studies has not only strict academic interest.

Table 1 Estimates of generic and species diversity of the most numerous families of freshwater mollusks of North and Central Europe made according the European and Russian taxonomic approaches. See also Graf (2007)

Family	European approach*		Russian approach**	
	Number of genera	Number of species	Number of genera	Number of species
Bithyniidae	1	5	4	12
Lymnaeidae	7	14	2	40
Planorbidae	9	21	9	61
Sphaeriidae	3	28	21	110
Unionidae	3	7	5	24
Valvatidae	2	6	3	31
Viviparidae	1	4	2	10

* Based on Falkner et al. (2001), Glöer (2002)

** Based on Starobogatov et al. (2004)

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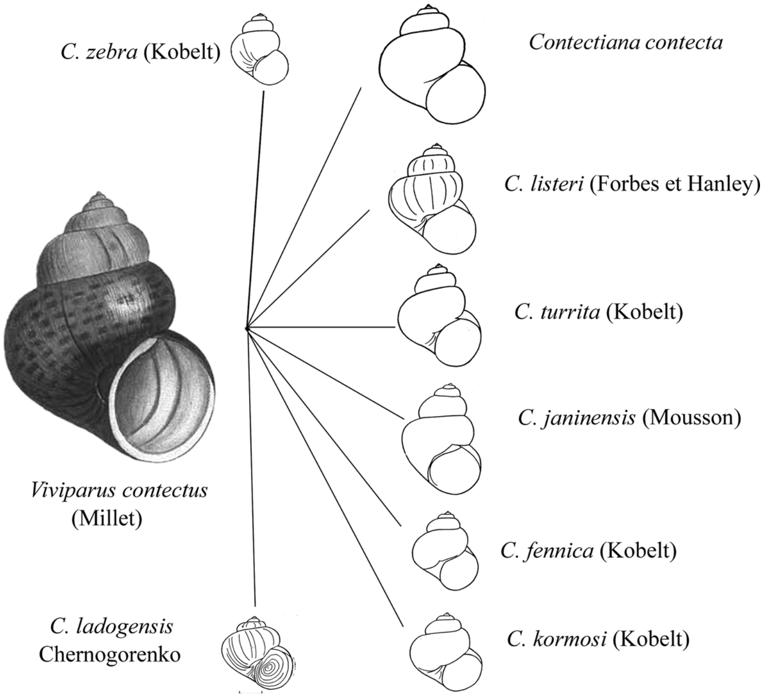

Fig. 1 Eight species from a single one. The species *Viviparus contectus* corresponds to eight species accepted in the Russian taxonomy. Shells of *Contectiana* after Chernogorenko (1988), shell of *V. contectus* after Küster (1852)

Materials and methods

Earlier, Vinarski et al. (2012a, b) used the Russian taxonomic approach in application to their study of the macroecological patterns of aquatic snails in Western Siberia. The general principles of compiling and processing the faunistic data are described in the abovementioned paper. Here, we tried to assess statistically the differences between patterns revealed by analysis of two independent datasets, generated in accordance with the European and the Russian approaches to freshwater mollusks systematics.

In order to do it, we "Europeanized" the dataset used by Vinarski et al. (2012a, b) by means of re-classifying all species of snails occurring in Western Siberia. The taxonomic position of each species included in the Vinarski et al. (2012a, b) database was determined anew following mainly Falkner et al. (2001) and Glöer (2002), with some changes based on recently published articles (Vinarski et al. 2011, 2012a, b) bringing the molecular support for validity of some "minor" species not recognized by the Western European authors. A table with full inventory of correspondences between taxonomic names accepted in Russia and their European counterparts is given in the Electronic Appendix. Several species of snails recently recorded from Western Siberian plain (see, for example, Vinarski 2011) and not included in the Vinarski et al. (2012a, b) database were omitted in our analyses.

Permissibility of such procedure is clear from the fact that most recent species of Gastropoda in Western Siberia have northern European origin and invaded this region in

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the Pleistocene and Holocene epochs (Starobogatov 1970; Vinarski et al. 2007, 2012a, b). Therefore Western European determination keys of freshwater mollusks contain a lot of species of Euro-Siberian or broadly Palearctic distribution (see, for example, Glöer 2002), and, hence, these keys are suitable for taxonomic identification of many species occurring in Siberia (except of Asiatic endemics, of course). Moreover, the taxonomic monograph by Zhadin (1952), published in the pre-Starobogatovian time, was based on the European taxonomic tradition, and for a long time it served as a main tool for identifying the Western Siberian species of aquatic mollusks.

As a result, we obtained two datasets in which values of three parameters of molluscan biological diversity in Western Siberia are accounted for twenty-four 1° latitudinal bands, from 50° to 73° of latitude (see Vinarski et al. 2012a, b). The total space of the area covered by the faunistic database is over 2500 km along the meridian. The three basic parameters calculated for each band are: total gastropod species richness (SR); portion of prosobranch species (belonging to the subclass Prosobranchia, or, in the Russian system, Pectinibranchia); and portion of species of non-European origin in the fauna. The second parameter reflects the arithmetical ratio between the number of prosobranch species and the overall SR in a latitudinal band; the third parameter was used by Vinarski et al. (2012a, b) for studying formation of the recent malacofauna of Western Siberia.

The focus of this study as well as of the previous work Vinarski et al. (2012a, b) is to characterize the latitudinal gradients of species richness and related diversity parameters in the Western Siberian region. The causal explanation of these gradients as well as the discussion of concrete cases of taxonomic discrepancies concerning delineation and naming of particular species were beyond the scope of our research.

We tried to determine whether there is significant difference between macroecological conclusions based on the Russian and European taxonomic frameworks. For that we applied the nonparametric Wilcoxon signed-rank test for paired comparisons. This test is designed for relatively small samples with unknown mode of distribution (distribution-free methods; Sokal and Rohlf 1995, pp. 440–450, Box 13.11). The evaluation of statistical significance of difference was carried out using the raw data. We assumed that though the Russian taxonomists operated with larger number of species but the species splitting effort made by them was nearly the same in all families of gastropods, therefore the two analyzed samples origin from the same entire assembly. Also, we performed a normalization of raw data for reducing between-sample variation in range of values.

For comparison of pairs of normalized data, the nonparametric Wilcoxon signed-rank test was also applied.

All statistical procedures were performed using software packages STATISTICA 6.0 (StatSoft Inc, USA) and PAST 3.01 (http://folk.uio.no/ohammer/past/).

Results

117 species of gastropods were identified under the Russian taxonomic framework and included in the Vinarski et al. (2012a, b) database (see Electronic Appendix). The "Europeization" of this database performed by us led to reducing this number to only 56 species, i.e. 2.09 times less. The cause of such strong decline is obviously different approaches to species delineation in the European and Russian taxonomic traditions with the latter being much more given to species splitting. For example, three species of acroloxid snails accepted in Russia (*Acroloxus lacustris*, *A. oblongus* and *A. shadini*) were treated by

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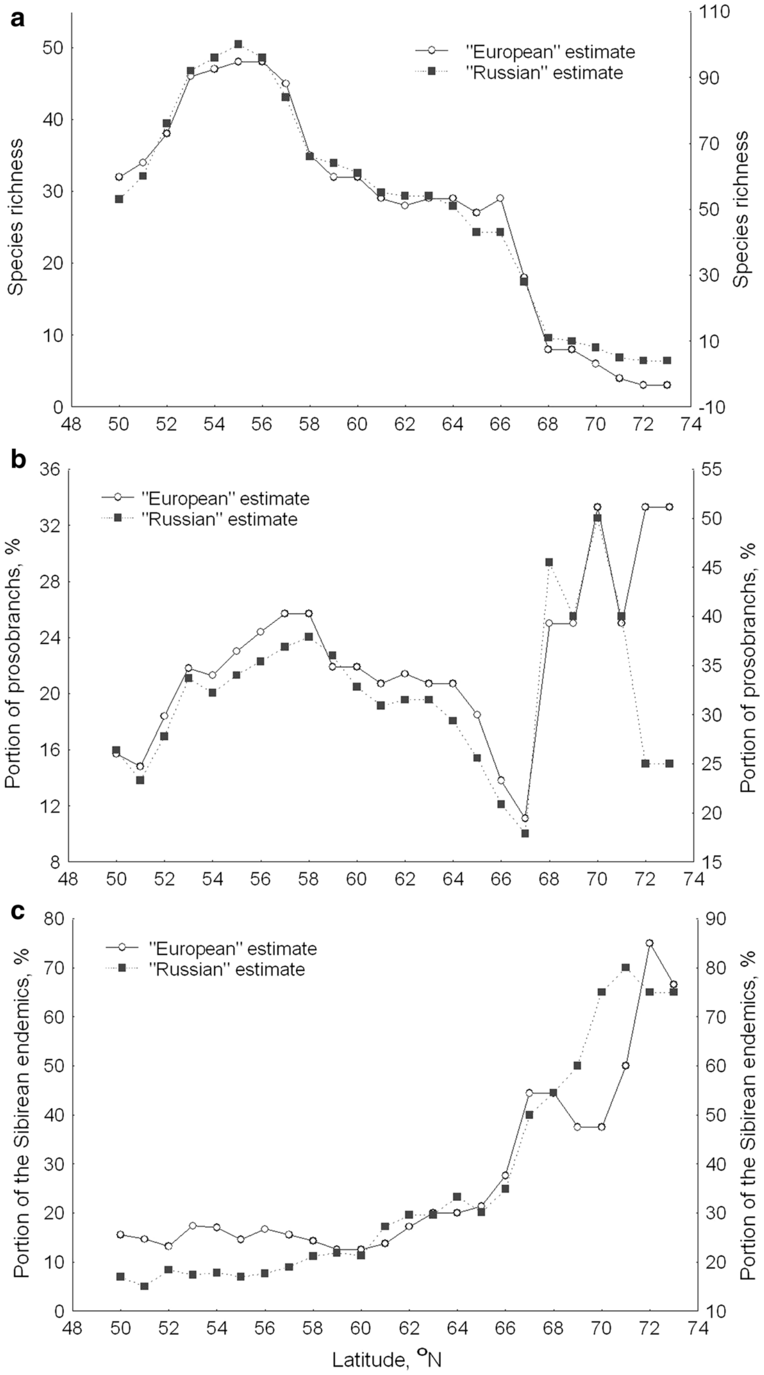

Fig. 2 Relationships between the three biodiversity parameters studied and geographical latitude in Western Siberia. **a** Species richness of gastropods. **b** Portion of branchiate gastropod species. **c** Portion of species of non-European (Siberian) origin

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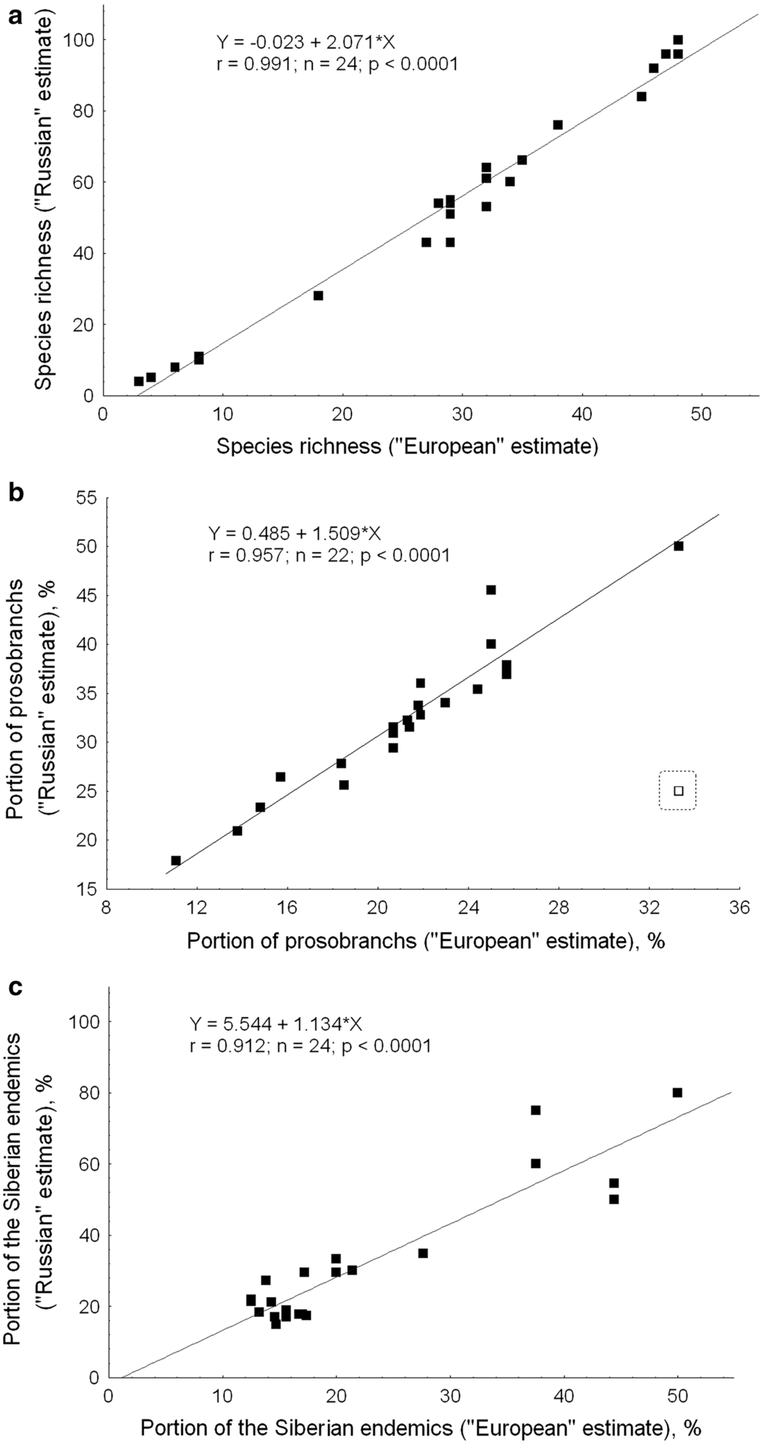

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◀**Fig. 3** Relationships between geographical latitude and **a** gastropod species richness, **b** portion of prosobranchs, and **c** portion of non-European species estimated by using the European and the Russian taxonomic frameworks

us as synonyms of a single species *Acroloxus lacustris* since the European authors did not accept the splitting of this species proposed by Kruglov and Starobogatov (1991). The number of Asiatic species that do not have exact correspondence with species listed in the Western Europeans handbooks appeared to be rather small (14 species out of 117) (see Electronic Appendix), and we believe this would not bias our results significantly.

The general shape of the relationship between SR and geographical latitude did not change when we switched to the European point of view (Fig. 2a). It is hump-backed (U-shaped), with clear peak between 54 and 57 degrees of latitude that corresponds in Western Siberia to the forest-steppe bioclimatic zone. High degree of resemblance between the lines is clearly seen also in two other graphs (Fig. 2b, c) though there is a strong dissimilarity between two estimates of the portion of prosobranch species in the extreme north latitudes (see Fig. 2b). It means that in all three cases the sequences of data may be mutually transformed by using the simple linear transformation.

Figure 3 shows that the initial and transformed sequences are strongly and significantly intercorrelated ($0.912 \leq r \leq 0.991$; in all cases $p < 0.0001$). The only exception is the difference in estimate of the portion of prosobranchs in the two northernmost latitudinal bands (see Fig. 2b). We excluded from our analyses the two points corresponding to these bands in order to avoid biased estimates.

The initial sequences of data corresponding to the European and the Russian taxonomic frameworks in all three cases were significantly different from each other, but after being linearly transformed these differences have disappeared (Table 2).

Discussion

The taxonomic uncertainty, especially at the species level, will, perhaps, never be avoided or eradicated (Hey et al. 2003), therefore ecologists and biogeographers should take this fact into account when studying large-scale patterns in organism diversity. On the other hand, the ghost of taxonomic bias is not always so harmful as it is occasionally assumed. The different views of systematists on the nature of biological species and diversity of opinions on how to delineate them are often cited as an essential source of troubles for end-users of the taxonomic information (Nazarenko 2001; Hey et al. 2003; Agapow et al. 2004; Jones et al. 2012). There is no general and commonly accepted species concept though we would mention a recent appeal to develop a certain *convention of species* to replace the plethora of particular species concepts rival to each other (Nazarenko 2001 but see Dubois 2011). Hausdorf (2011) outlines a generalized species concept grounded on the fundamental biological properties of this taxonomic rank. The very possibility of such attempts is explained by the fact that the species are real and objective entities, therefore even highly dissimilar approaches to their delimitation will bring somewhat comparable results. The "lumpers" and the "splitters" should deal with fundamentally the same set of organisms destined to be classified by means of their distribution among primary taxonomic units known as "species". It is impossible to ignore the most important biological characteristics of animals although it remains a matter of choice how to "weigh" them taxonomically.

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Table 2 Results of the comparison of initial and normalized data sequences by means of the nonparametric Wilcoxon signed-rank test

Parameter	n	Initial data	Normalized data
Species richness	24	$Z = 4.286$; $p < 0.0001$	$Z = 0.486$; $p = 0.627$
Portion of prosobranchs	22	$Z = 4.107$; $p < 0.0001$	$Z = 0.536$; $p = 0.592$
Portion of non-European species	24	$Z = 4.107$; $p < 0.0001$	$Z = 0.371$; $p = 0.710$

In the studied case, taxonomically biased data are not powerful enough to qualitatively alter macroecological patterns in a widely distributed and species-rich group of aquatic invertebrates. It is a good example of relatively low harmful taxonomical splitting though, at first sight, it may seem the double increase in number of accepted species would seriously alter the large-scale patterns in snail diversity.

The comparatorial method used for species delimitation by the Leningrad School was applied consistently to all families of freshwater snails, both branchiates and pulmonates (Chernogorenko 1988; Kruglov and Starobogatov 1991; Starobogatov et al. 2004; and many others). Korniushin (1998) established a simple conformity between the Russian taxonomic approach and the traditional one: "each genus or subgenus of the former corresponds to a certain species of a group of closely related species of the latter" (see also Graf 2007). Some (not numerous) exceptions from this conformity rule discussed by Korniushin (1998, 2002) apply to bivalves. In snails, the correspondence between the two taxonomic frameworks is much more regular. As a result, the "splitting process" initiated by the founder of the Leningrad School run more or less evenly in all families of freshwater gastropods subjected to taxonomic revision in the works of Starobogatov and his disciples and followers. It is worthy to note here that taxonomic splitting as such is not methodologically "worse" than taxonomic lumping since both approaches may produce valuable results. For example, some "minor" species of aquatic snails resurrected from lists of synonyms by the Leningrad School, proved to be real after careful examination including study of the type series (Vinarski and Glöer 2008; Glöer and Georgiev 2014).

The practical implications of our case study are twofold:

1. One should not to acclaim a priori that the discrepancies among systematists will automatically distort macroecological inferences or alter them qualitatively. In every case of doubts, a quantitative test of possible effects must be carried out.
2. To estimate the magnitude of a possible bias caused by taxonomic uncertainty, species overdescription or other factors and to predict its probable influence one has to examine the methodological foundations that resulted in development of competitive taxonomic frameworks. In addition to the case of the comparatorial method described above, one may recall the introduction of the phylogenetic species concept in the early 1980s (Cracraft 1983) that brought to a dramatic growth in number of accepted species in many animal taxa, for example, in fish (Mina et al. 2006) and birds (Nazarenko 2001). We would predict, however, that the consistent use of this concept instead of, for example, once dominated BSC, may not influence large-scale patterns similar to those studies in this work.

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