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Mechanisms of fast transformations of Baikal biota: multidisciplinary approach

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ABSTRACT. We discuss the current state of investigations concerning the impact of dramatic ecosystem rearrangements in Lake Baikal on the evolution of the lake's biota, as well as the approaches that should be used to achieve further progress in this area.

Keywords: evolution, modelling, climate change, Lake Baikal

It is difficult to find more compatible entity than Lake Baikal with long-term stability of environment (Grachev et al., 1998; Kuzmin et al., 2001; MacKay, 2007). High variability of the crucial natural conditions defining physical ecological niches and continuous environmental challenges are the major factors of survival of all components of this giant and ancient eco-system (Sherbakov, 1999; Dynesius and Jansson, 2000 etc.). Therefore, fast and dramatic transformations of the physical conditions should influence significantly the evolutionary processes of the biotic component of the lake ecosystem. Moreover, the environmental oscillations of such scale are important per se and require specific adaptations of organisms (Margalef, 1978). Fig.1 shows possible evolutionary consequences of environmental oscillations indicating that the different rates and spans of morphological evolution may cause different outcomes ranging from speciation to the development of a generalist species.

Unfortunately, the role of fast environmental changes as the force formning the evolution of Baikal biota has been underestimated and understudied until now in spite of the availability of excellent paleontological record providing firm evidences of its importance (Grachev et al., 1998; Kuzmin et al., 2001; Karabanov et al., 2004). On the other hand, the problems concerning long and short term consequences of dramatic environmental processes in Lake Baikal become increasingly important scientifically and attract attention of general public due to the last events, including blooming of filamentous green algae (Romanova et al., 2013; Kravtsova et al., 2014) and spreading sponge disease (Khanaev et al., 2018; Kulakova et al., 2018).

Any study aimed at the elucidation of evolution-

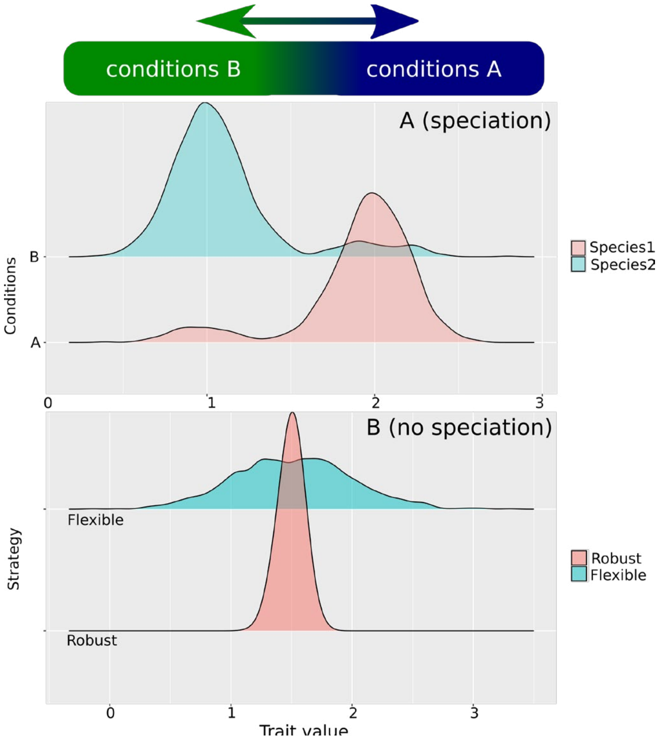

Fig. 1. Different evolutionary consequences of oscillating environment. Horizontal bar at the top shows to sets of conditions between which the oscillation of environment occurs. A: the case of speciation of a single common ancestor (not shown) splits into two sister specialist species adapted to the opposite conditions but able to survive unfavourable periods; B: the two cases when the oscillations do not cause speciation due to the contrasting adaptation strategies. The flexible (upper curve) strategy causes evolution towards single species of extreme morphological diversity similar to the case described by Johnson and Stankowski (2018), the second strategy is a selection of robust specialist able to survive the extreme conditions.

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ary mechanisms, which make complex assemblages of organisms sustaining the challenges offered by global and/or local processes, must be multidisciplinary. Now, we are going to adopt different points of view at the most crucial problems concerning the sustainability mechanisms of the Baikal biodiversity with respect to the stream of environmental challenges it used to face so successfully until now.

Classic ecological and hydro-biological approaches are indispensable, both in justification of new studies and in the previous knowledge about the ecosystem. Taking into account almost perfect isolation of Baikal species from the neighbouring biotopes, one may speculate that the rate of species description from the lake should decrease from now on, and the taxonomy of major groups should reach saturation. This means that the past century period of extensive study of the lake (Timoshkin, 1997) is about to be finished, and the main focus will shift towards the organization of organisms at higher levels, and future findings should be expected in the field of organismal interactions in such complex communities typical for Lake Baikal.

Indeed, to date 34 distinctive species communities of macroinvertebrates have been described in the Southern Basin of the lake. These communities are dominated by amphipods, oligochaets, trichopterans, chironomids, mollusks and representatives of other groups. Species diversity of all communities is high: their Shannon index varies from 2.9 to 4. Number of species forming invertebrate communities range from 36 to 144 species, and from 5 to 17 of them may dominate by biomass that is evidence of a complex structural organization of the communities (Kravtsova et al., 2004). This complexity suggests high stability. However, it is still not clear, if they remain stable during evolution. One may expect that if inter-specific interactions are taken into account, the picture will become even more complicated. No wonder that some peculiarities in general setup communities in Lake Baikal had been already described, but they had to be explained. Moreover, coevolution between most species in communities has not proved yet.

Analysis of the coordination between evolutionary processes in species belonging to the same community means that the complexity of data analysis increases dramatically in comparison with "mere" description of biological phenomena. Therefore, more sophisticated methods of data analysis and statistical assessments are required. Theoretical treatment of evolutionary problems becomes increasingly important. The most common theoretical approach includes some kind of modelling of processes studied in a way that the result of modelling repeats the experimental data used. This approach was developed as early as in 2004 (Semovski et al., 2004a; Bukin et al., 2007; Fazalova et al., 2010) and used successfully to elucidate several cases of complex micro-evolutionary events that generated peculiar molecular phylogenies. Fig. 2 show one of these examples. Individual-based model was used to show that the Fst metrics designed to describe pair-wise differentiation between populations; it is still useful in case of many populations. Application of this approach is justified for the description of population subdivision of *Gmelinoides fasciatus* (Gomanenko et al., 2005; Bukin et al., 2018). The same approach was effective in case of demographic changes of population. It allowed estimating the number of sequences for elucidation of a real-world problem (Semovski et al., 2004a; 2004b). In all simulations, the environmental changes were modelled as changes of "environmental capacity", which was defined as the maximum number of individuals sustained at biotope under given conditions. Fig. 2 shows the individual-based modelling of genetic differentiation between four linear populations of organisms with different mobility (average distance of migration from the birthplace). In further studies, the modelling approach will be applied to newer kinds of data, such as multiple SNPs and microsatellite loci, which will be added to the individual characteristics of objects.

In general, new possibilities in studies of biodiversity appeared, when high throughput DNA sequencing techniques became feasible for environmental and/or evolutionary studies of invertebrates, protists and algae (Sauvadet et al., 2010; De Vargas et al., 2015; Leray and Knowlton, 2015). Additionally, the diversity of protists in nature was underestimated significantly, and metagenomics approach was absolutely necessary for describing biodiversity (Leray and Knowlton, 2016). Species composition of protists was shown to be very specific. The study of eukaryotic metagenomes is es-

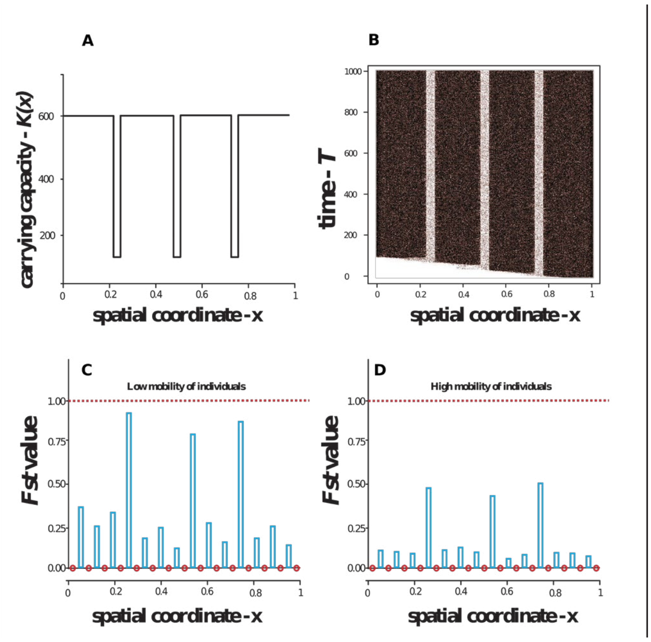

Fig. 2. The semi-transparent barriers between the populations arranged as shown on the panel A. Panel B shows the initial expansion of the individuals (each dot corresponds to an individual) filling the whole range and forming the distribution stabile in time. Semi-transparent barriers between the populations are much less densely populated. Red circles on panels C and D designate sampling points along the spatial coordinate (x). Fst values were calculated by splitting the simulated data into two sets left and right from every stretch linking neighbouring "sampling points". Panel C shows Fst peaking on the barriers in case of low organism mobility, D - the same in case of high organism mobility. The simulation illustrates that Fst may be useful for finding barriers between more than two populations.

pecially important, since recently occurring fast local transformations in Lake Baikal changed environment of near-shore zone of the lake most likely due to antropogenic impact, although natural reasons cannot be fully eliminated (Kravtsova et al., 2014). One of the most obvious features of the changes is bloom of filamentous green algae in many cases dominated by species of *Spirogyra* (Romanova et al., 2013). Representatives of this genus were described as very rare species in Lake Baikal in the middle of the 20th century (Izhboldina, 2007). It is important to understand, whether the current blooming is caused by the local opportunistic species responding to the favourable conditions, or by the exotic species that invaded Lake Baikal. Unfortunately, it is difficult to rely on morphologically-based species diagnoses due to lack of morphological traits in this group (Wongsawad and Peerapornpisal, 2015).

Our preliminary metagenomic data suggest that there are, in fact, several sequences of *Spirogyra* possibly of the species rank, and at least some of them are very close to non-Baikal species (in press).

Notably, the application of modern methods of high throughput sequencing in studies of Baikal biota have begun relatively recently (Ravin et al., 2010). Studies in this direction have revealed many unexpected findings, some of which are difficult to explain (Romanova et al., 2016; Kulakova et al., 2018). For instance, an extremely high level of gene order rearrangements in mitochondrial genome (as exemplified in Fig. 3) in comparison with the non-Baikal sister taxa (Cormier et al., 2018).The most rearranged mitochondrial genome was detected in shallow water amphipods *Gmelinoides fasciatus*. This finding appears to be especially mysterious in combination with the data on extreme longevity and evolutionary stability of amphipods species (Bukin et al., 2018). The habitat of this amphipod species was affected in thecourse of global ecosystem changes through the whole history of a large lake within the confines of current Baikal. In spite of dramatic ecosystem transformations, this species has survived and kept its identity.

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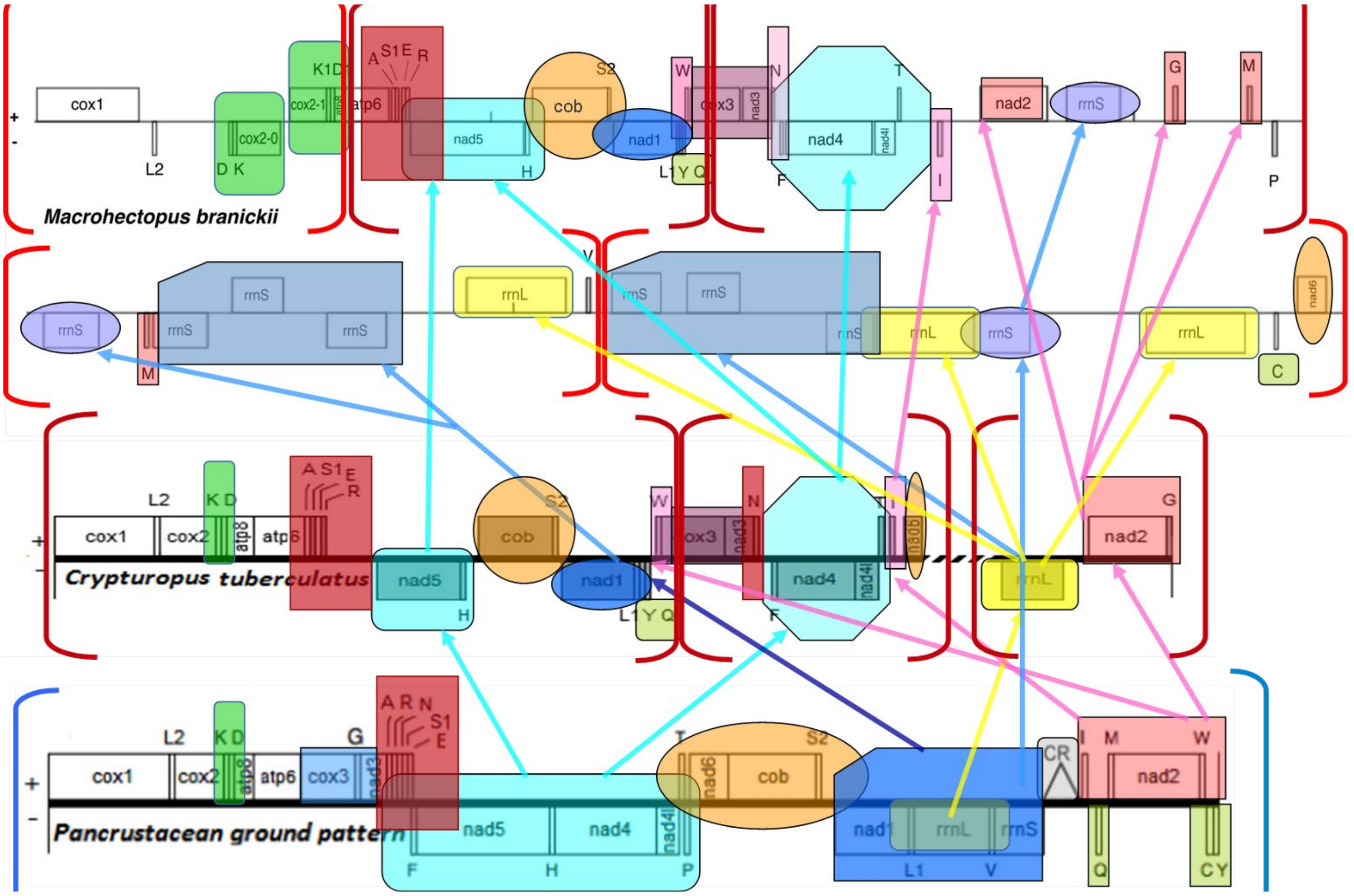

Fig. 3. Gene order rearrangements in Baikal amphipods *Crypturopus tuberculatus* and *Gmelinoides fasciatus* compared to the Pancrustacean ground pattern shared among most of Crustacea.

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