

Native *Dreissena* freshwater mussels in the Balkans

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Native *Dreissena* freshwater mussels in the Balkans: in and out of ancient lakes

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Abstract

The Balkans is a biogeographically highly diverse region and a worldwide hotspot of endemic freshwater diversity. A substantial part of this diversity is attributed to well recognized and potential ancient lakes in its southwestern part. Despite considerable research efforts, faunal relationships among those lakes are, however, not well understood. Therefore, genetic information from native representatives of the mussel genus *Dreissena* is used here to test the biogeographical zonation of the Southwestern Balkans, to relate demographic changes to environmental changes, to assess the degree of eco-insularity, to reconstruct their evolutionary history, and to explore the potential of native taxa for becoming invasive.

Phylogeographical and population genetic analyses indicate that most populations studied belong to two native species: *D. presbensis* (incl. the distinct genetic subgroup from Lake Ohrid, *D. "stankovici"*) and *D. blanci*. In addition, the first confirmed record of invasive *D. polymorpha* in the Southwestern Balkan is presented. The distribution of native *Dreissena* spp. is largely in concordance with the biogeographical zonations previously proposed based on fish data. Disagreement, however, consists regarding the assignment of the ancient lakes in the area to biogeographical regions. The data for Lake Ohrid are not conclusive. For Lake Prespa, however, a closer biogeographical connection to lakes of the Vardar region and possibly the Northern Ionian region is suggested. While reconstructing the evolutionary histories of *Dreissena* spp., signs of major demographic and spatial expansions were found. They started some 320 000–300 000 years ago in *D. "stankovici"*, some 160 000–140 000 years ago in *D. blanci*, and some 110 000–70 000 years ago in *D. presbensis*. These time frames are discussed within the context of available paleogeological data for lakes Ohrid and Prespa. It is suggested that regional environmental changes may have had pronounced effects on the population histories of native *Dreissena* spp., though the high buffer capacity of Lake Ohrid may have mitigated these effects in *D. "stankovici"*. In addition, local events acting upon individual lakes very likely had considerable effects on the demographic

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histories of *Dreissena* spp. as well. The observed patterns of immigration and emigration in and out of ancient lakes may suggest that limited gene flow supported the survival of small isolated subpopulations, while eco-insularity may have prevented excessive hybridization and sympatry of closely related taxa.

As for the potential invasiveness of native *Dreissena* spp., the significant spatial expansions inferred are not human-mediated and all taxa still appear to be restricted to their native ranges. Of concern, however, is that *D. presbensis* and *D. blanci* today also occur in artificial water bodies, and that invasive *D. polymorpha* has reached the area.

1 Introduction

The Balkans, a mountainous area in Southeastern Europe, have long been recognized as a worldwide hotspot of endemic freshwater biodiversity (Radoman, 1985; Banarescu, 1991; Griffiths et al., 2004; Strong et al., 2008). This high degree of biodiversity, particularly in invertebrates, has been attributed to (i) the role of the Balkans as one of the major European Pleistocene refugia (e.g., Deneffe et al., 2000; Tzedakis, 2009; Lezine et al., 2010), (ii) its rich geological history, for example, the upheaval of various mountain ranges, the interplay of Tethys and Paratethys, and the former contact to Anatolia (Radoman, 1985; Banarescu, 1991), (iii) its various biogeographical zones (Banarescu, 2004), and (iv) its high diversity of freshwater habitats ranging from cold springs, glacial lakes and mountain streams to ephemeral rivers and extended lake systems, including a number of actual or potential ancient lakes. In fact, the South-western Balkans arguably harbour all ancient lakes in Europe, except for the Caspian Sea (Albrecht and Wilke, 2008; also see Fig. 1).

These lakes comprise ancient Lake Ohrid, situated in the Former Yugoslav Republic of Macedonia (from hereon called Macedonia) and the Republic of Albania (from hereon called Albania), as well as Lake Prespa (Macedonia, Greece, Albania). In addition, there are less known, potential ancient lakes such as lakes Skutari (Montenegro, Albania), Mikri Prespa (Greece, Albania), Pamvotis (Greece), Vegorititis (Greece), Dojran (Macedonia, Greece), and Trichonis (Greece). As ancient lakes often have

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continuously existed for hundred thousands or even million years, and as they can harbour a high degree of endemic faunal elements, they are popular systems for reconstructing faunal relationships and changes of species composition in space and time (e.g., Martens, 1997).

5 Knowledge about the latter once remains limited for the Balkan ancient lakes, thus hampering a better understanding of the link between geography and faunal evolution of lacustrine faunas in the Balkans in general. Parts of the problem are an uneven scientific coverage of the different water bodies in the area with a strong bias to the ancient lakes Ohrid and Prespa (reviewed in Albrecht and Wilke, 2008) and, to a lesser extent, to lakes Trichonis (e.g., Albrecht et al., 2009), Pamvotis (e.g., Frogley and Preece, 10 2004), Skutari (e.g., Karaman and Beeton, 1981), and Dojran (e.g., Griffiths et al., 2002; Reed, 2004). More importantly, despite recent attempts to enhance our understanding of biogeographical processes on a regional scale (Griffiths and Frogley, 2004; Korniusin, 2004; Lipej and Dulčić, 2004; Reed, 2004; Hauswald et al., 2008), our 15 knowledge of patterns of freshwater biogeographical zonation in the Balkans remains largely biased towards fishes and drainage networks (e.g., Banarescu, 2004). According to these data, the Southwestern Balkans are bordered by the Danube River Basin to the north and by the Adriatic Sea, the Mediterranean Sea and the Aegean Sea to the west, south and east, respectively. The Southwestern Balkans themselves consist 20 of the following biogeographical regions: the Dalmatian region in the northwest, the Macedonia-Thessaly region in the north, the South Adriatic-Ionian region in the west, the Thrace region in the northeast, as well as the Attiko-Beotia region in the southeast. This zoogeographical division largely corresponds to the “ecoregions” suggested by Abell et al. (2008) (see Fig. 1).

25 Despite minor differences in the corresponding regions, both divisions place lakes Ohrid and Prespa in the Southeastern Adriatic Drainage/South Adriatic-Ionian region. Banarescu (1991: 751), however, specifically acknowledged the faunal distinctness of Lake Ohrid “...its fauna has however a number of peculiarities and cannot be considered as only a subdivision of the large West Balkan ...”.

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The affiliation of both lakes to the Southeastern Adriatic drainage region, and particularly the close biogeographical relationships between the two lakes remains controversial (reviewed in Albrecht and Wilke, 2008). In fact, a cluster analysis of 147 mollusc species from all major natural lakes in the Southwestern Balkans (Albrecht et al., 2009) indicated that Lake Ohrid is highly distinct with relatively little faunal overlap to neighbouring Lake Prespa. The latter lake, in turn, appears to be more closely related to lakes of the Vardar region (lakes Vegoritits and Dojran), and not to the lakes of the Southeastern Adriatic and Ionian drainages (lakes Skutari, Pamvotis, Amvrakia, Trichonis; but see Albrecht et al., 2008).

So far, there are no conclusive explanations as to the low degree of faunal exchange (immigration and emigration) between Lake Ohrid and neighbouring water systems. Radoman (1985) suggested an inherent structure of the biocoenosis that prevents such events; the well adapted endemic organisms of Lake Ohrid may out-compete most invading species but are probably inferior outside native Lake Ohrid – a pattern called eco-insularity (Boss, 1978).

Over the past years, a number of molecular studies have used species-level phylogenetic relationships as indirect evidence for faunal exchange of Lake Ohrid (e.g., Albrecht et al., 2006, 2007, 2008; Wilke et al., 2007; Hauswald et al., 2008; Schultheiß et al., 2008; Wysocka et al., 2008; Trajanovski et al., 2010a). In contrast, population-genetic studies remain scarce (e.g., Sell and Spirkovski, 2004).

The problem is of circular nature: for studying immigration and emigration in ancient lakes within a population-level context, one ideally would need a single species or a set of closely related species with a Balkan-wide distribution. However, due to the high degrees of eco-insularity and endemism in these ancient lakes with corresponding low degrees of immigration and emigration, only few such candidate species exist.

A potential exception are the closely related Southwestern Balkan representatives of the freshwater mussel genus *Dreissena* Van Beneden, 1835.

The genus has become infamous because of two highly invasive representatives, the zebra mussel *D. polymorpha* (Pallas, 1771) and the quagga mussel *D. rostriformis bugensis* (Andrusov, 1897), which are considered pest species in large parts of North America (e.g., May and Marsden, 1992; Nalepa and Schloesser, 1993) and Europe (e.g., Kinzelbach, 1992; Molloy et al., 2007). Though the occurrence of at least one of these invasive species, *D. polymorpha*, in the Southwestern Balkans has been noted repeatedly (reviewed in Albrecht et al., 2007), recent studies strongly suggest that, so far, only native species of *Dreissena* occur in the area (e.g., Stepien et al., 2003; Gelembiuk et al., 2006; May et al., 2006; Albrecht et al., 2007). The latter workers could show that these native representatives are closely related, all belonging to the subgenus *Carinodreissena*. The southern parts of the area are inhabited by *D. blanci* Westerlund, 1890, which has originally been described from the Lake Trichonis area. The workers could also show that the second native species, nominal *D. stankovici* L'vova and Starobogatov, 1982, supposedly endemic to Lake Ohrid, is not restricted to the ancient lakes Ohrid and Prespa, but that it is a widespread taxon in the northern part of the area. As nominal *D. blanci* f. *presbensis* Kobelt, 1915 described from Lake Prespa has nomenclatural priority over *D. stankovici* described from Lake Ohrid, the correct name for the latter taxon should be *Dreissena presbensis*. However, strictly for didactical reasons, we here use the name *D. "stankovici"* for the genetic subgroup primarily associated with Lake Ohrid, and *D. presbensis* for the genetic subgroup primarily associated with Lake Prespa.

Interestingly, specimens of *D. blanci* and *D. presbensis* occur sympatrically in lakes Prespa and Pamvotis. Given the close relationship of native Balkan *Dreissena* spp. and their relatively wide distribution, we here utilize genetic information from 269 specimens within a system of phylogeographical and population genetic analyses to:

- test the biogeographical zonation in the Southwestern Balkans in respect to the regions previously described for the area,
- relate demographic changes in *Dreissena* spp. to environmental changes,

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- assess the degree of eco-insularity and reconstruct the evolutionary history of *Dreissena* spp., and
- explore the potential of these native taxa for becoming invasive.

2 Materials and methods

2.1 Specimens studied

The current study comprises samples of *Dreissena* spp. from 47 localities (Table 1) in the Central and Southwestern Balkans, covering 13 larger natural and artificial water bodies (important limnological characteristics of natural lakes are given in Table 2). In addition, 11 other major water bodies were sampled, but did not yield specimens of *Dreissena* spp.: the Mavrovo, Globocica, and Strezevo reservoirs (Macedonia); lakes Kastorias, Petron, Chimaditis, Pikrolimni, Koronia, Lysimachia, and Ozeros, as well as the Kerkini Reservoir (all Greece). Field work was conducted between 2003 and 2009.

Our sampling encompasses all nominal *Dreissena* taxa from the area (see Bank, 2006; Albrecht et al., 2007), including materials from or close to their respective type localities: *D. stankovici* L'vova and Starobogatov, 1982 (type locality Lake Ohrid), *D. blanci* Westerlund, 1890 (= *D. chemnitzii* Westerlund and Blank, 1879; = *D. hellenica* Locard, 1893; = *D. thiesae* Locard, 1893; type localities all Missolonghi), and *D. blanci presbensis* Kobelt, 1915 (type locality Lake Prespa).

2.2 DNA isolation and sequencing

The method described in Wilke et al. (2006) was used for isolating DNA from individual mussels. The primers for amplifying a fragment of the cytochrome *c* oxidase subunit I (COI) gene with a target length of 658 base pairs (bp), excluding 51 bp of primer sequence, were LCO1490 and HCO2198, as described by Folmer et al. (1994). Sequences (forward and reverse) were determined using the LI-COR (Lincoln, NE, USA) DNA sequencer Long ReadIR 4200 and the Thermo Sequenase fluorescent labelled primer cycle sequencing kit (Amersham Pharmacia Biotech, Piscataway, NJ,

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USA). The protein-coding mitochondrial COI sequences, which are free of insertions and deletions in *Dreissena*, were aligned unambiguously by eye using BioEdit 7.0.8.0 (Hall, 1999). The first few base pairs behind the 3' end of each primer were difficult to read. We therefore uniformly cut off the first and last 10 bp of each sequence, leaving a 638-bp-long overlapping fragment for the COI gene. All sequences are available from GenBank (accession numbers EF414478–EF414492, EF414496, HM209829–HM210081).

2.3 Phylogeographical history and summary statistics

2.3.1 Network analyses

A statistical parsimony haplotype network was constructed utilizing the program TCS 1.21 (Clement et al., 2000), with the connection limit set to 95% and gaps being treated as fifth state. Network ambiguities were resolved according to the criteria of Pfenninger and Posada (2002). In a second analysis, we reduced the connection limit to 90% (=15 mutational steps) in an attempt to infer the connection among sub-networks. In a third analysis, we analyzed our three taxa individually for inferring the respective ancestral haplotypes.

2.3.2 Test for genetic structure

In order to reconstruct the demographic and spatial history of *Dreissena* spp., we first tested for significant genetic structure within those taxa that did not exceed the 95% connection limit of the network analysis (see Result section).

We performed a hierarchical Analysis of Molecular Variance (AMOVA) with a distance matrix of pairwise differences and tested the significance of the Φ statistic by generating a null-distribution based on 10 000 permutations of the original dataset utilizing Arlequin 3.5.1.2. (Excoffier et al., 2005). Hierarchical grouping variables were (i) taxa, (ii) lake systems, (iii) populations.

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As an alternative approach for studying genetic differentiation among taxa, we performed an exact test as suggested by Raymond and Rousset (1995) and implemented in Arlequin 3.5.1.2. The assumed null hypothesis of the test statistics is a random distribution of different haplotypes among populations (i.e. panmixia). The significance of differentiation between taxa was evaluated by running the Markov chain for 1 000 000 steps.

2.3.3 Tests for neutrality

In order to test for the effects of past demographic events (i.e. changes in population size) or influences of selection in *Dreissena* spp., we utilized Tajima's (1989) *D* statistic as implemented in Arlequin 3.5.1.2. Significances of the statistic were inferred using coalescent simulations with 10 000 replicates.

2.3.4 Testing models of demographic and spatial expansions

Demographic and spatial histories of populations were inferred by linking the amount and distribution of sequence differences to relative time since divergence, utilizing mismatch analyses. While a demographic equilibrium, that is, constant population size, generates a multimodal distribution of pairwise nucleotide differences, a demographic expansion is indicated by a unimodal distribution (Rogers and Harpending, 1992). Schneider and Excoffier (1999) and Excoffier (2004) extended this approach, allowing for the estimation of demographic parameters from demographic and spatial expansion models based on a generalized non-linear least-square approach.

First, we tested the spatial expansion model for the three taxa *Dreissena* "*stankovici*", *D. presbensis*, and *D. blanci*. In contrast to the demographic expansion model, this model does not require panmixia but assumes that the sampled group is subdivided into an infinite number of demes exchanging migrants (i.e. restricted gene flow between groups). Then, we tested the model of demographic expansion in each of the three taxa. As this model requires panmixia and as this assumption was violated in all taxa due to a significant genetic structuring of individual lakes in the AMOVA (except

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for *D. "stankovici"*), we used for this test only specimens from that lake system that presumably constitutes the source for subsequent spatial expansion of the respective taxon (see Results section for details). These are for *D. "stankovici"* Lake Ohrid, for *D. presbensis* Lake Prespa, and for *D. blanci* Lake Trichonis. Confidence intervals (CI) for both models were estimated based on coalescent simulations with 10 000 replicates.

2.3.5 Estimation of time since population expansion

Mismatch analyses also allow for estimating τ , a population parameter that enables the calculation of time since expansion. With $\tau=2tu$, t is the time in generations and u is the total mutation rate μ per generation (Rogers and Harpending, 1992; Schneider and Excoffier, 1999). In the absence of a *Dreissena*-specific substitution rate for the COI gene, we here utilize the trait specific COI Protostomia molecular clock rate of $1.22\% \pm 0.27\%$ substitutions per site and one million years for the Jukes-Cantor model (Wilke et al., 2009). This rate has been shown to be robust among invertebrate taxa with similar biological and life-history characteristics (i.e. dioecious tropical or subtropical taxa with a generation time of ~ 1 year and a body size of approximately 2–50 mm). All these criteria are met by *Dreissena* spp. from the Balkans.

In order to provide meaningful confidence intervals for our time estimates, we here account for both the error of the τ estimate ($\Delta\tau$; see Table 5) and the error of the mutation rate ($\Delta\mu$, here $0.27\% \text{ Ma}^{-1}$, see above). For doing so, we calculate the propagation of uncertainty based on the partial derivatives of the underlying function (i.e. $t=\tau*2u^{-1}$). Following Rogers and Harpending (1992: 562), u equals $m_T\mu$, where m_T is the number of base pairs in the fragment under consideration (here: 638 bp) and μ is the substitution rate per nucleotide (here $1.22\% \text{ Ma}^{-1}$). Hence, the function (without errors) is:

$$T(\tau, \mu) = \frac{\tau}{2m_T\mu}. \quad (1)$$

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Using the partial derivatives of this function, we then can calculate the total error of the time estimate as follows:

$$\Delta T = \sqrt{\left(\frac{\partial G}{\partial \tau} \Delta \tau\right)^2 + \left(\frac{\partial G}{\partial \mu} \Delta \mu\right)^2} = \sqrt{\left(\frac{1}{2m_{\tau}\mu} \Delta \tau\right)^2 + \left(\frac{\tau}{2m_{\tau}\mu^2} \Delta \mu\right)^2}. \quad (2)$$

Error calculations were carried out utilizing the R software environment (R Development Core Team, 2007).

3 Results

3.1 Network analyses

The first analysis resulted in three distinct sub-networks that exceeded the 95% connection limit. Sub-network I comprises all haplotypes of native *Dreissena presbensis*, including those of *D. "stankovici"*, sub-network II all haplotypes of native *D. blanci*, and sub-network III the single haplotype of invasive *D. polymorpha* (Fig. 2).

The *D. blanci* sub-network consists of 55 specimens with 17 haplotypes, 10 of them shared (Fig. 2). According to the network analysis, the taxon occurs allopatrically in the southern water bodies Trichonis, Amvrakia, Stratos and Kastrakiou, and, in low frequencies, sympatrically with *D. presbensis* in the central lakes Pamvotis and Prespa as well as in the Aliakmonas Reservoir (Fig. 1). The highest haplotype diversity and the highest ratio of private haplotypes (i.e. haplotypes only occurring in a single water body) are found in Lake Trichonis.

The *D. presbensis*/*D. "stankovici"* sub-network encompasses 211 specimens with 105 haplotypes (58 for *D. "stankovici"* and 47 for *D. presbensis*), 16 of them shared (7 and 9, respectively).

Haplotypes of *D. "stankovici"* (lakes Ohrid and Skutari) are completely separated from *D. presbensis* haplotypes from lakes Pamvotis, Prespa, Mikri Prespa, Vegoritis, Dojran, and Volvi as well as the Aliakmonas Reservoir (Figs. 1 and 2). The two groups

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are, however, separated by only one mutational step. The highest haplotype diversity and the highest ratio of private haplotypes for *D. "stankovici"* are to be found in Lake Ohrid; for *D. presbensis* in Lake Prespa.

When reducing the connection limit of the network analysis to 90% in order to infer the link between sub-networks, an almost direct connection between the most common haplotype in *D. "stankovici"* (haplotype S1 in Fig. 2) and the most common haplotype in *D. blanci* (B1) becomes evident. The *D. polymorpha* sub-network, however, remains disconnected. The individual network analyses of the three native taxa suggested the following ancestral haplotypes: *D. "stankovici"*, haplotype S6 (biggest outgroup probability 0.127); *D. presbensis*, haplotype P1 (biggest outgroup probability 0.116); *D. blanci*, haplotype B1 (biggest outgroup probability 0.256).

The potential ancestral haplotype in *D. "stankovici"* (S6) constitutes a central haplotype within this taxon and it is shared by specimens of lakes Ohrid and Skutari. Lake Ohrid, however, is considered to be the ancestral area for the extant haplotypes of *D. "stankovici"* as it has a higher diversity of haplotypes and a higher ratio of private haplotypes. The putative ancestral haplotype for *D. presbensis* (P1) also represents a central haplotype within this taxon. It is only shared by specimens from Lake Prespa and the small neighbouring Lake Mikri Prespa. As Lake Prespa, however, has a much higher total number of private haplotypes and as most of these haplotypes are derived from the putative ancestral haplotype P1, Lake Prespa appears to be the ancestral area for all extant haplotypes of *D. presbensis*. For *D. blanci*, the inferred ancestral haplotype is haplotype B1. As Lake Trichonis is the only natural lake in which this haplotype has been found during our survey (accept for a single specimen in Lake Prespa), and as this lake shows the highest number of private *D. blanci* haplotypes, it is assumed to be the ancestral area for the extant diversity of *D. blanci*.

3.2 Test for genetic structure

We performed two AMOVAs, corresponding to the two major sub-networks obtained in the first network analysis (see Fig. 2): *D. presbensis*+*D. "stankovici"* and *D. blanci*.

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The first analysis revealed a highly significant amount of genetic differentiation between *D. presbensis* and *D. "stankovici"* with 33.45% of the total variation being distributed between these two groups ($F_{CT}=0.3345$, $p<0.05$). Following the qualitative guidelines of Wright (1978), this fixation index indicates high genetic differentiation. Variation among populations within groups accounted for 20.45% of total variation ($F_{SC}=0.3073$, $p<0.001$) and variation within populations for 46.10% of total variation ($F_{ST}=0.5390$, $p<0.001$).

Whereas a pairwise comparison of lakes did not indicate significant differences in the genetic structure of *D. "stankovici"* (i.e. between lakes Ohrid and Skutari; $p=0.106$), differentiation among water bodies harbouring specimens of *D. presbensis* were mostly significant (Table 3).

The alternative exact test of sample differentiation based on haplotype frequencies also rejected the global null hypothesis of panmixia of *D. presbensis* and *D. "stankovici"* from a total of 9 water bodies ($p<0.001$).

The analysis of *D. blanci* indicated that in this taxon, variance among populations accounted for 24.02% of total variation and variation within populations for 75.98% ($F_{ST}=0.2402$, $p<0.001$). Note that among-group-variation is not applicable as this analysis involved only a single taxon. Results of pairwise comparisons among water bodies, being mostly significant, are given in Table 4.

The alternative exact test of sample differentiation based on haplotype frequencies also rejected the global null hypothesis of panmixia of *D. blanci* from a total of 7 water bodies studied ($p<0.001$).

3.3 Tests for neutrality

Tajima's *D* test of selective neutrality showed a significant deviation from the neutral mutation hypothesis in all three taxa (*D. presbensis*: $D=-2.43$, $p<0.001$; *D. "stankovici"*: $D=-2.42$, $p<0.001$; *D. blanci*: $D=-1.54$, $p=0.025$). Together with negative *D*-values, this indicates population size expansion and/or positive selection.

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3.4 Testing models of demographic and spatial expansions

All individual mismatch analyses (Fig. 3) showed a unimodal distribution of pairwise nucleotide differences (also see the corresponding low raggedness values in Table 5, which are all non-significant). In addition, all sum of squared deviation (SSD) values (Table 5) are very low as well, none of them being significant. These data indicate that neither the pure demographic expansion model for lakes Ohrid, Prespa and Trichonis, nor the spatial expansion model for *D. "stankovici"*, *D. presbensis*, and *D. blanci* are rejected in favour of a demographic equilibrium.

3.5 Estimation of time since population expansion

The mean time estimates for the beginning of spatial/demographic expansion in *D. "stankovici"*, *D. presbensis*, and *D. blanci* are given in Table 5. The demographic expansion of *D. "stankovici"* in Lake Ohrid and its spatial expansion into Lake Skutari started some 320 000–300 000 years ago and therefore considerably earlier than the demographic expansion of *D. presbensis* within Lake Prespa and its spatial expansion into nearby water bodies some 110 000 and 70 000 years ago, respectively (also see the non-overlapping CI's in Table 5). The demographic expansion of *D. blanci* and its spatial expansion out of Lake Trichonis (160 000 and 140 000 years ago, respectively) apparently started before the spread of *D. presbensis*, but considerably later than the expansions of *D. "stankovici"* (CI's, however, are overlapping). The spatial expansion of *D. presbensis* out of Lake Prespa appeared to have started considerably later than its demographic expansion (but CI's are overlapping).

It should be noted that the onsets of population expansions inferred here for *Dreissena* spp. are independent of the age of the respective most recent common ancestors (MRCA). Judging from the mismatch distributions in Fig. 3, the age of the MRCA in all three taxa may be considerably higher than the inferred age of spatial expansion.

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4 Discussion

4.1 Biogeographical zones on the Southern Balkans

The biogeographical zonation of *Dreissena* spp. here inferred from molecular data is largely in concordance with the zonations previously proposed based on data from fishes. *Dreissena* “*stankovici*” exclusively occurs in the ecoregion “Southeastern Adriatic drainages” (Fig. 1), *D. blanci* mainly in the ecoregion “Ionian drainages”, and *D. presbensis* mainly in the Vardar and Thrace ecoregion. Considerable disagreement consists, however, regarding the assignment of the ancient lakes Ohrid and Prespa to ecoregions. Most workers consider Lake Ohrid to belong to the Southeastern Adriatic drainages (see Introduction, also see Albrecht and Wilke, 2008). Some workers noted a relationship to the Ionian region (e.g., Wilke et al., 2007), yet other workers point to the high degree of isolation and faunal distinctness of Lake Ohrid faunal elements, possibly warranting the assignment to an own region (e.g., Banarescu, 1991; Albrecht et al., 2009; Hauffe et al., 2010; Trajanovski et al., 2010a). The data presented here, indeed, indicate a close relationship of Lake Ohrid specimens to the ecoregion “Southeastern Adriatic drainages”, demonstrated by the occurrence of *D. “stankovici”* in Lake Skutari. As the latter lake, however, is almost directly connected to Lake Ohrid via the Drim River, the relatively isolated occurrence of *D. “stankovici”* in the Skutari area should not be overrated. Less ambiguous is the situation of Lake Prespa. While most workers consider this lake to be biogeographically closely related to Lake Ohrid, recent studies (e.g., Albrecht and Wilke, 2008; Albrecht et al., 2009) suggest a closer biogeographical connection between Lake Prespa and the lakes of the Vardar region. The latter pattern is also supported by the genetic analyses presented here. We therefore suggest modifying the borders of the Vardar ecoregion to include lakes Prespa and Mikri Prespa (also see Marková et al., 2010).

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4.2 Demographic changes in *Dreissena* spp. relative to environmental changes

While the distribution of groups of species among ecoregions often reflects the general biogeographical history of a larger area, a comparison of closely related taxa may reveal the affects of small-scale biotic and abiotic factors in space and time.

5 Estimations of the timing of population changes have revealed that the onsets of demographic and spatial expansions in the three native taxa do not coincide, but differ considerably in time. This raises the question as to whether environmental changes (e.g. recovery from catastrophic lake-level low stands; Sturmbauer et al., 2001; Schultheiß et al., 2009) may have triggered population expansions, and if so, 10 whether these changes were of global, regional, or local nature. Acknowledging that these different spatial scales may not be mutually exclusive, the disconcordance of demographic events in the taxa studied might, at first sight, point to local effects acting upon individual lakes and their respective species. The situation, however, appears to be more complex due to the fact that different lakes with different limnological characteristics (e.g. size, depth, source of water, residence time of water; also see Table 2) 15 may buffer environmental changes at different degrees.

Unfortunately, we are unable to provide explanations for the population expansions in *D. "stankovici"* some 300 000–320 000 years ago and in *D. blanci* some 140 000 years ago due to lack of relevant paleolimnological data. The demographic expansion of 20 *D. presbensis* in Lake Prespa some 110 000 years ago, however, can possibly be linked to environmental and climatic fluctuations that were inferred for the Ohrid-Prespa region during the last glacial-interglacial cycle (Lindhorst et al., 2010; Vogel et al., 2010a, b; Wagner et al., 2010). The Eemian interglacial ended roughly 110 000 years ago and was characterized by abrupt climatic changes and significant lake level fluctuations 25 (Lezine et al., 2010), which might have caused the observed demographic expansion. Interestingly, while these affects are apparent in Lake Prespa, they did not leave traces in the demographic history of *D. "stankovici"* in Lake Ohrid. In fact, a recent study shows that during the Last Interglacial, *D. "stankovici"* already had a dominant position

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in the benthic invertebrate assemblages of the latter lake (Albrecht et al., 2010). These observations lead to the hypothesis that regional environmental changes may have had pronounced effects on the population histories of *Dreissena* spp. in the Balkans, though the high buffer capacity of, for example, Lake Ohrid (deep oligotrophic lake with a considerable water input coming from sublacustrine springs) may have mitigated these effects (but see Reed et al., 2010 for the sensitivity of diatoms to climate change in Lake Ohrid). Thus, the onset of spatial expansion in *D. presbensis* out of Lake Prespa may be associated with a recovery from lake level low stands, while we do not see such effects in Lake Ohrid populations. Nonetheless, given the patchy distribution of lakes in the area, local events acting upon individual lakes very likely had pronounced effects on the respective demographic histories of *Dreissena* spp. as well. In fact, both the exact test of sample differentiation and the AMOVA reject panmixia within the three native taxa studied. The high degree of genetic structure in all these taxa is rather unexpected. Most water bodies studied here are frequently used by migratory water birds as breeding or resting grounds (e.g., Grimmett and Jones, 1989). Together with the, in part, low geographical distance among these water bodies, one would expect a high degree of passive dispersal and therefore considerable gene flow among lakes and reservoir. The AMOVA's, however, indicate significant pairwise genetic differences among *D. presbensis* populations from different water bodies, except for lakes Pamvotis, Dojran and the Aliakmonas Reservoir (Table 3). The same is true for *D. blanci*. Within this taxon, populations from different water bodies show a high degree of pairwise differentiation except for those inhabiting the Aliakmonas Reservoir and Lake Trichonis (Table 4). While both taxa have a relatively high number of private haplotypes in natural lakes (particularly in ancient lakes), we only see in *D. presbensis* a clear geographical structure (Fig. 2). Most specimens from lakes Prespa and Mikri Prespa form one group, specimens from remote Lake Pamvotis form a second group, and most specimens from the eastern lakes and reservoirs (Vegoritits, Dojran, Volvi, Aliakmonas) form a third group. The difference in geographical structure between *D. presbensis* and *D. blanci* could, however, be simple the result of an isolation-by-distance effect as

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D. blanci has a much smaller range than *D. presbensis* (see Fig. 1).

4.3 Faunal exchange and eco-insularity of ancient lakes in space and time

While isolation-by-distance may explain some of the patterns observed in our data set, it does not explain the lack of faunal overlap between lakes Prespa and Ohrid. While haplotypes of *D. "stankovici"* and *D. presbensis* differ by as little as one mutational step (see Fig. 2), neither do these sister-lakes share haplotypes nor do individual haplotypes from Lake Ohrid cluster together with those from Lake Prespa. The high degree of eco-insularity in ancient lakes also becomes evident when looking at the distribution of haplotypes (particularly private haplotypes) among water bodies. The highest haplotype diversities and the highest ratio of private haplotypes (see Fig. 1) are to be found in (i) Lake Ohrid, (ii) Lake Prespa, and (iii) Lake Trichonis. Interestingly these lakes also appear to be, possibly in the same order, the oldest lakes in the Balkans (e.g., Albrecht and Wilke, 2008; Albrecht et al., 2009). Acknowledging that we are unable to provide a quantifiable neutral model of private haplotype diversities, we do see a general trend showing an increase of haplotype diversities from artificial and relatively young natural lakes over potential ancient lakes to well recognized ancient lakes, such as Lake Ohrid. In other words, the degree of eco-insularity may be related to the age of the respective water body and it is well conceivable that species in those lakes, characterized by long demographic histories, are better adapted to the individual settings of ancient lakes and that they are therefore able to typically out-compete immigrants originating from other water bodies (see Boss, 1978; Radoman, 1985). Moreover, it has recently been shown for the Neogene lakes in the Balkans that, once a fauna evolved in situ, inter-lake exchange remains extremely rare (Harzhauser and Mandic, 2008). Of course, isolation (and therefore the frequency of emigration and immigration events) also plays an important role for eco-insularity. In fact, long-lived lakes (ancient lakes and paleolakes) have repeatedly been regarded as islands with patterns observed being discussed in an island-biogeographic context (e.g., Wesselingh, 2007).

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We do not know the processes leading to the relative high degree of eco-insularity of *Dreissena* spp. in ancient lakes in the Balkans but empirical evidence from aquarium experiments (Wilke et al., unpublished data) also indicate that *D. "stankovici"* from Lake Ohrid is extremely hard to maintain outside its native environment. This double-sided affect of eco-insularity – endemic organisms may outcompete most invading species but are probably inferior outside their native water bodies – may have considerable implications for the protection of native *Dreissena* spp. on the Balkans. As shown by Trajanovski et al. (2010b), Lake Ohrid harbours an increasing number of invasive species. These species are mainly to be found in environmentally disturbed areas such as the eutrophicated Ohrid Bay on the Macedonian side and the Lin Peninsula on the Albanian side (also see Matzinger et al., 2007). There, water conditions might have changed in a way that endemic species lose their competitive advantage. These are therefore the areas specimens from outside could populate most easily and from where a displacement of native populations could start. The first confirmed record of *D. polymorpha* in the Southwestern Balkans presented here comes from such a disturbed system – from Lake Saško in the Skutari drainage.

Our data also indicate that immigration and emigration of *Dreissena* specimens may occur on a regular basis in the Balkans. This becomes evident not only from specimens found in relatively young artificial water bodies such as the Aliakmonas, Kastrakiou and Stratos reservoirs (Fig. 1), but also from the low-frequency-occurrence of *D. blanci* specimens in lakes Pamvotis and Prespa.

4.4 Evolutionary history of native *Dreissena* spp. in the Balkans

Some dispersal events may, however, result in small isolated subpopulations subject to severe bottle necks and subsequent genetic drift (Wright, 1931; Wilke et al., 2010). These processes could, at least partly, explain the patterns of extant *Dreissena* biodiversity seen in the Balkans. Given that these native taxa form a monophyletic group as suggested by Albrecht et al. (2007), and considering their demographic histories and patterns of haplotype diversity inferred in the present paper, we suggest that an

ancestral *Dreissena* population in Lake Ohrid may be the source of today's *Dreissena* biodiversity in the area.

Specimens of this population possibly invaded lakes in the Southern Ionian region, such as Lake Trichonis, and became reproductively isolated (extant *D. blanci*). Independent of this event, and probably during a later point in time, specimens of the ancestral source population also invaded Lake Prespa (extant *D. presbensis*). After a major demographic expansion, Lake Prespa then probably became the source for the spreading of *D. presbensis* to lakes in the Vardar and Thrace regions. Given the close haplotype relationship of *D. presbensis* from lakes Prespa and Pamvotis (see, for example, the shared haplotype P5 in Fig. 2), Lake Prespa possibly constituted the source for *D. presbensis* specimens in Lake Pamvotis (Ionian region) as well.

Interestingly, there also has been a spread of specimens of *D. "stankovici"* from Lake Ohrid into the Skutari system. This is, however, not surprising as the only outflow of Lake Ohrid, the Drim River (see Fig. 1), runs along Lake Skutari. In fact, a similar "out of Ohrid" event has been noted by Wilke et al. (2007). In their paper, the workers presented data suggesting that the ancestor of the pyrgulinid gastropod species *Pyrgula annulata*, which today occurs in some Italian lakes, in Croatia and also in Lake Skutari, probably inhabited Lake Ohrid. Studies on the endemic cypriniform fish fauna also suggest a closely interlinked Ohrid-Drim-Skutari system (Šanda, 2007; Talevski et al., 2009; Marková et al., 2010).

The patterns of (limited) immigration and emigration observed here may help providing a hypothesis for the high degree of freshwater biodiversity in the Balkans not only for *Dreissena* spp., but also for other invertebrate taxa. We suggest that during an early limnological phase (or after catastrophic limnological events), a patchy system of ancient lakes in the area with limited gene flow supported the survival of small isolated subpopulations. Probably during a later phase, eco-insularity of lake faunas prevented excessive hybridization and sympatry of closely related taxa. Future studies focusing on processes such as selection vs. drift based on additional nuclear markers may help testing this hypothesis.

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4.5 Potential of native *Dreissena* spp. in the Balkans for becoming invasive

Given that the two well-known invasive *Dreissena* taxa, *D. polymorpha* and *D. rostriformis bugensis* probably started their massive spreading in western Europe and North America out of small isolated areas and that the native *Dreissena* species in the Balkans are now known to occur in many more water bodies than previously believed, there is a real concern that one or more of these native taxa could become invasive (see Albrecht et al., 2007). The data presented here, however, indicate that their spatial expansion already started between some 70 000 and 300 000 years ago and therefore is not human-mediated. Moreover, all species still appear to be restricted to their native ranges. Of concern, however, is that two taxa, *D. presbensis* and *D. blanci*, today also occur in artificial water bodies. While many reservoirs in the area are still free of *Dreissena* spp. (see the negative records in Fig. 1), we did find specimens in large abundances in at least three major reservoirs situated in two ecoregions. We therefore urgently suggest a monitoring program of *Dreissena* spp. in artificial lakes in the area as an early warning system. At the same time, studies are necessary investigating whether invasive *D. polymorpha* show signs of further range expansions into areas currently exclusively populated by native *Dreissena* taxa in the Balkans.

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Table 1. Locality information for specimens of *Dreissena* spp. studied, including drainage system, latitude and longitude information (in decimal degrees N and W, respectively), as well as DNA isolation numbers and respective haplotype information for individual specimens (in parentheses).

Drainage system	Latitude	Longitude	DNA isolation number of individual specimens (haplotype number)
<i>Dreissena polymorpha</i>			
Skutari (Saško Lake)	41.97679	19.33871	12852 (Pol), 12853 (Pol), 12855 (Pol)
<i>Dreissena "stankovici"</i>			
Ohrid	41.10508	20.78048	3960 (S7), 4157 (S9), 4158 (S1), 4189 (S13), 4190 (S14), 4654 (S34)
Ohrid	41.16074	20.68662	4159 (S10), 4191 (S1), 4192 (S15), 4249 (S21), 4287 (S25), 4288 (S26)
Ohrid	41.16267	20.68716	4294 (S29), 4295 (S30), 4296 (S32), 4297 (S32), 4298 (S33)
Ohrid	41.11485	20.64473	3961 (S8), 4161 (S5), 4162 (S11), 4193 (S16), 4194 (S17), 4663 (S3), 4664 (S36)
Ohrid	41.08714	20.79424	4163 (S12), 4164 (S3), 4195 (S18), 4291 (S28), 4657 (S35), 4658 (S3)
Ohrid	41.01626	20.63430	4701 (S37), 4702 (S38), 4703 (S39), 4704 (S40), 4705 (S6), 4706 (S41)
Ohrid	40.97324	20.78668	4171 (S2), 4172 (S1), 4203 (S19), 4204 (S20), 4289 (S5), 4290 (S27)
Ohrid	40.91363	20.73756	4911 (S51), 4912 (S52), 4914 (S53), 4916 (S4), 4917 (S54), 4918 (S5)
Ohrid	40.97301	20.64445	4895 (S46), 4896 (S6), 4897 (S47)
Ohrid	41.03023	20.63521	4887 (S1), 4888 (S42), 4889 (S43), 4891 (S3), 4892 (S44), 4893 (S45)
Ohrid	40.98652	20.79818	3967 (S2), 4281 (S22), 4282 (S23), 4283 (S24), 4284 (S1), 4285 (S2), 4286 (S2)
Skutari	42.23	19.13	4903 (S4), 4905 (S4), 4906 (S4), 4908 (S48), 4909 (S49), 4910 (S50)
Skutari	42.35862	19.10630	12845 (S6)
Skutari	42.16695	19.22564	12847 (S25), 12849 (S58), 12850 (S56)
Skutari	41.98523	19.43216	12833(S57), 12834 (S25)
Skutari	42.00598	19.60028	12835 (S55), 12838 (S6)
<i>Dreissena presbensis</i>			
Aliakmonas	40.48620	22.25767	9185 (P8), 9186 (P2), 9188 (P9), 9189 (P43), 9191 (P44), 9192 (P9), 9193 (P4)
Dojran	41.21873	22.77928	4571 (P24)
Dojran	41.18786	22.7231	9304 (P8), 9306 (P2), 9307 (P45), 9308 (P46), 9313 (P2)
Mikri Prespa	40.75589	21.10273	4469 (P14), 4470 (P1), 4471 (P1), 4473 (P1), 4474 (P15)
Mikri Prespa	40.69718	21.03827	4475 (P1), 4478 (P1), 4479 (P1), 4480 (P1)
Mikri Prespa	40.79296	21.07416	4481 (P1), 4482 (P1), 4483 (P1), 4485 (P1), 4486 (P1)
Mikri Prespa	40.69718	21.03827	4647 (P1), 4649 (P1)
Mikri Prespa	40.79296	21.07416	4650 (P6), 4651 (P1)
Mikri Prespa	40.75589	21.10273	4652 (P1)

Table 1. Continued.

Drainage system	Latitude	Longitude	DNA isolation number of individual specimens (haplotype number)
Pamvotis	39.68320	20.86954	4575 (P3), 4661 (P3), 4662 (P3)
Pamvotis	39.68872	20.84427	4642 (P3), 4643 (P3), 4644 (P3), 4645 (P3), 4646 (P25)
Pamvotis	39.67827	20.87722	4683 (P28), 4684 (P5), 4685 (P3), 4686 (P3), 4687 (P3), 4688 (P29)
Prespa	40.87103	20.98772	3966 (P10), 4275 (P1), 4276 (P1), 4277 (P1), 4278 (P13), 4280 (P1)
Prespa	40.93665	20.94414	3964 (P1), 4165 (P1), 4166 (P1), 4167 (P11), 4197 (P1), 4198 (P1), 4199 (P12)
Prespa	40.93828	20.94855	4168 (P1), 4169 (P1), 4170 (P1), 4200 (P1), 4201 (P1), 4202 (P1)
Prespa	40.76848	20.92642	4813 (P1), 4814 (P30), 4815 (P1), 4816 (P31), 4817 (P7), 4818 (P32), 4829 (P6), 4830 (P1), 4831 (P1), 4832 (P1), 4833 (P34), 4834 (P1)
Prespa	40.86210	20.94061	4821 (P7), 4822 (P1), 4823 (P1), 4824 (P1), 4826 (P1), 4827 (P33), 4839 (P1), 4840 (P35), 4841 (P1), 4842 (P36), 4843 (P37), 4844 (P38)
Prespa	40.99446	20.93346	4845 (P39), 4846 (P1), 4847 (P1), 4848 (P40), 4849 (P41), 4850 (P1)
Prespa	40.82032	21.01939	4503 (P5), 4505 (P16), 4506 (P5), 4507 (P17), 4510 (P18)
Prespa	40.83677	21.02141	4511 (P1), 4512 (P19), 4514 (P20), 4515 (P21), 4516 (P22), 4518 (P23)
Vegoritis	40.71857	21.74950	4572 (P2), 4573 (P2), 4574 (P2)
Vegoritis	40.78619	21.81685	4665 (P26), 4666 (P2), 4667 (P27), 4668 (P2)
Vegoritis	40.79	21.82	5169 (P42), 5171 (P2), 5172 (P2), 5201 (P2), 5203 (P2), 5204 (P2), 5205 (P2)
Volvi	40.67561	23.56736	9264 (P4), 9265 (P2), 9266 (P2), 9267 (P2), 9268 (P2), 9269 (P4), 9270 (P4), 9271 (P2), 9272 (P2), 9273 (P2)
Volvi	40.67565	23.56322	9314 (P47), 9316 (P2), 9317 (P2)
<i>Dreissena blanci</i>			
Aliakmonas	40.48620	22.25767	9184 (B1), 9187 (B2), 9190 (B2)
Amvrakia	38.76788	21.16916	4790 (B3), 4791 (B3), 4793 (B5), 4794 (B3), 4795 (B3), 4796 (B3)
Kastrakiou	38.82002	21.33194	9164 (B1), 9165 (B6), 9166 (B7), 9167 (B8), 9168 (B2), 9169 (B4), 9170 (B1), 9171 (B6), 9172 (B9), 9173 (B8), 9274 (B2), 9275 (B17), 9276 (B5), 9277 (B6), 9279 (B1)
Pamvotis	39.68320	20.86954	4576 (B10)
Prespa	40.82032	21.01939	4508 (B1)
Stratos	38.67126	21.34027	9174 (B1), 9175 (B4), 9176 (B17), 9177 (B2), 9178 (B5), 9179 (B9), 9180 (B1), 9181 (B4), 9182 (B1), 9183 (B7), 9678 (B4), 9679 (B2), 9680 (B4), 9681 (B5), 9682 (B5), 9684 (B9), 9685 (B6)
Trichonis	38.55133	21.53817	4773 (B2), 4775 (B11), 4776 (B12), 4777 (B13), 4778 (B2), 4779 (B14)
Trichonis	38.52763	21.65608	4781 (B2), 4782 (B15), 4784 (B1), 4785 (B16), 4787 (B2), 4788 (B1)

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Table 2. Summarized physiographical and hydrological characteristics of large natural lakes in the Southwestern Balkans from which specimens of *Dreissena* spp. were obtained.

	Lake Ohrid ¹	Lake Skutari ²	Lake Prespa ¹	Lake Trichonis ³	Lake Vegorit ³	Lake Volvi ³	Lake Mikri Prespa ¹	Lake Dojran ³	Lake Pamvotis ³	Lake Amvrakia ³
Altitude (m a.s.l.)	693	10	849	18	524	37	853	145	470	16
Surface area (km ²)	358	500	254	96.5	53	68	53	43	22	14.2
Maximum length (km)	30.3	44	27.3	18.2	11.0	20.2	14.3	8.0	7.8	6.2
Maximum width (km)	15.6	13	17.0	7.5	5.2	6.7	6.5	5.9	4.6	3.3
Maximum depth (m)	289	8	58	58	29	23	8.4	10.4	11	37
Mean depth (m)	155	6.8	14	30.3	70	13.8	4.1	5.5	5.5	4.4
Volume (km ³)	55	4.0	3.6	2.9	1.53	0.94	0.22	0.32	0.12	0.06
Watershed area (km ²)	1002	5500	~1000	421	1,853	220	260	420	330	177
Retention time (years)	70	0.3	25	9.4	9.5	–	28	–	0.8	9.4

¹ Albrecht and Wilke, 2008

² Royal Haskoning, 2006

³ Zacharias et al., 2002; length and width calculated from GoogleEarth, ©2010 Google

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Table 3. Results of AMOVA test of significant pairwise genetic differences (level 0.05) in *Dreissena presbensis* from different water bodies.

	Lake Prespa	Lake Mikri Prespa	Lake Pamvotis	Lake Vegoritis	Lake Dojran	Lake Volvi
Lake Prespa						
Lake Mikri Prespa	+					
Lake Pamvotis	+	+				
Lake Vegoritis	+	+	+			
Lake Dojran	+	+	–	+		
Lake Volvi	+	+	+	+	+	
Aliakmonas Reservoir	+	+	–	+	–	+

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Table 4. Results of AMOVA test of significant pairwise genetic differences (level 0.05) in *Dreissena blanci* from different water bodies. Note that lakes Prespa and Trichonis were excluded from the analysis as only a single specimen each was sampled in these lakes.

	Lake Trichonis	Lake Amvrakia	Kastrakiou Reservoir	Stratos Reservoir
Lake Trichonis				
Lake Amvrakia	+			
Kastrakiou Reservoir	+	+		
Stratos Reservoir	+	+	+	
Aliakmonas Reservoir	–	+	+	+

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Table 5. Estimated parameters of spatial and demographic expansion models in native *Dreissena* spp. based on mismatch analyses. For details on the estimation of time since expansion and its confidence intervals see the Method section. SSD: sum of squared deviations from the respective model; p: significance of the respective parameter; RI: raggedness index; τ : population parameter Tau; CI: 95% confidence interval; T : time since population expansion.

	Spatial expansion model			Demographic expansion model		
	<i>D. "stankovici"</i> (all sites)	<i>D. presbensis</i> (all sites)	<i>D. blanci</i> (all sites)	<i>D. "stankovici"</i> (Lake Ohrid)	<i>D. presbensis</i> (Lake Prespa)	<i>D. blanci</i> (Lake Trichonis)
SSD (p-value)	0.001 (0.53)	0.001 (0.60)	0.001 (0.80)	0.002 (0.26)	0.001 (0.95)	0.009 (0.73)
RI (p-value)	0.016 (0.61)	0.024 (0.80)	0.019 (0.88)	0.018 (0.28)	0.019 (0.98)	0.039 (0.80)
τ	4.63	1.12	2.24	5.02	1.76	2.48
(CI)	(2.96–5.12)	(0.69–3.16)	(1.29–3.68)	(4.18–5.70)	(0.43–3.80)	(1.05–5.83)
T in Mya	0.297	0.072	0.144	0.322	0.113	0.160
(CI)	(0.201–0.393)	(0–0.153)	(0.061–0.227)	(0.236–0.409)	(0.002–0.224)	(0.002–0.317)

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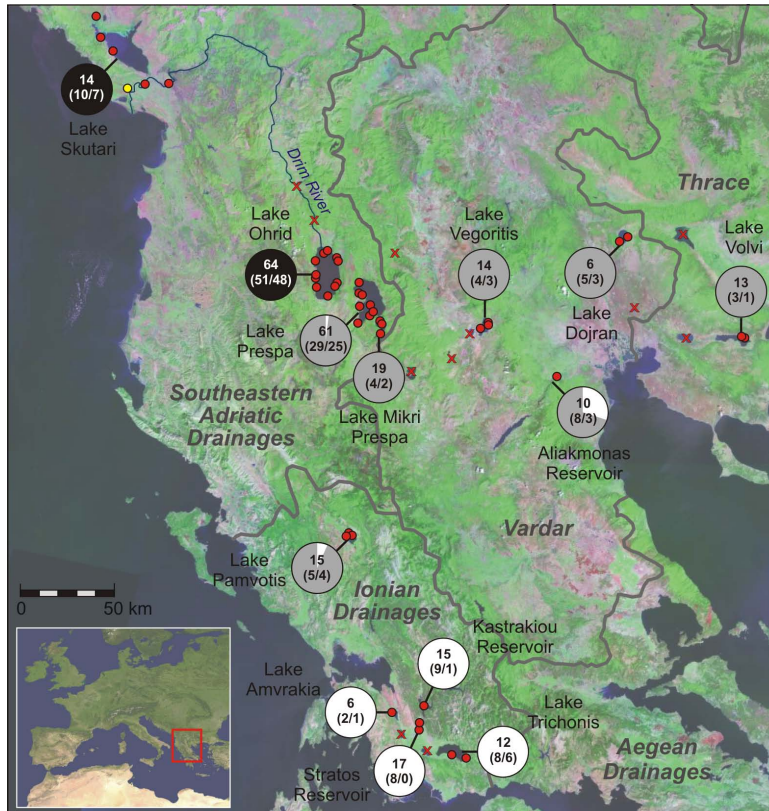


Fig. 1. Map of the Southwestern Balkans showing the water bodies sampled for *Dreissena* spp. Records for native species are shown as red dots, for invasive species as yellow dot (for detailed locality information see Table 1). Negative records of *Dreissena* spp. are indicated by the x-symbol. Distribution of genetic groups of native species within the water bodies studies are indicated by coloured pie diagrams (black: *D. stankovici*, gray: *D. presbensis*, white: *D. blanci*). Note that this assignment is a result of the present study. Numbers indicate total number of specimens studied for each water body (upper line) as well as the total number of haplotypes/private haplotypes found (lower line in parentheses). Major ecoregions are derived from Abell et al. (2008) and indicated by solid gray lines and italic names. Base map adapted from Mountain High Maps®, Copyright© 1993, Digital Wisdom®, Inc.

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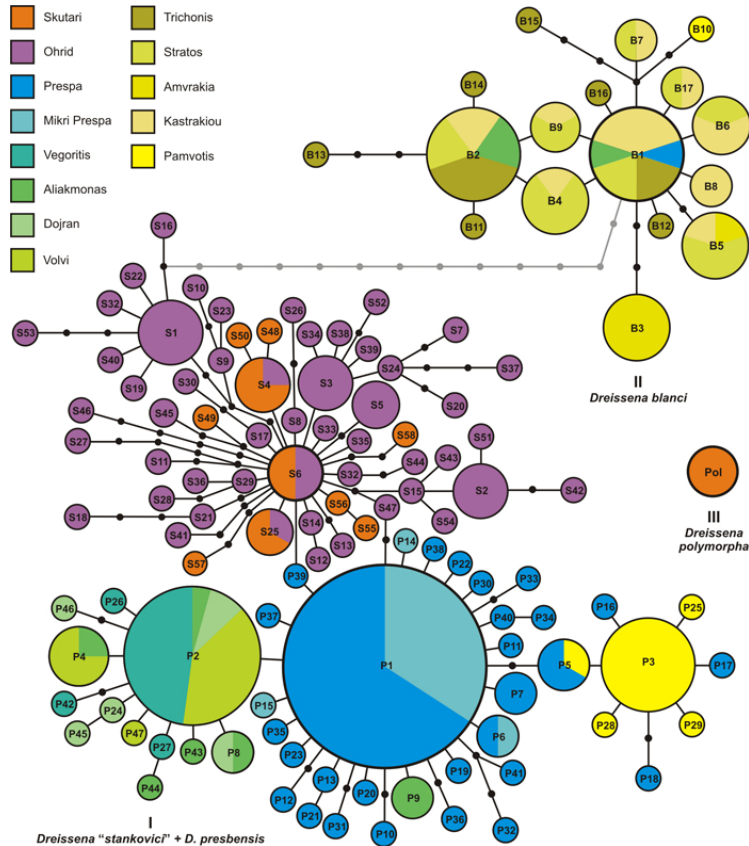


Fig. 2. Statistical parsimony haplotype network of *Dreissena* spp. based on COI mtDNA data (connection limit 95%). Haplotypes are colour-coded according to major lake systems (see Table 1 for detailed locality information). Areas of circles representing the haplotypes found are proportional to the number of specimens sharing the respective haplotype (for an assignment of haplotypes to individual specimens and their exact locations see Table 1; Pol=*D. polymorpha*, S=*D. "stankovici"*, P=*D. presbensis*, B=*D. blanci*). Missing haplotypes are indicated by black dots. The gray line shows the connection between *D. "stankovici"* and *D. blanci* when reducing the TCS connection limit to 90%. Haplotypes with the highest probability of being the ancestral haplotypes in the four taxa studied are indicated by bold circles (see Method section for details).

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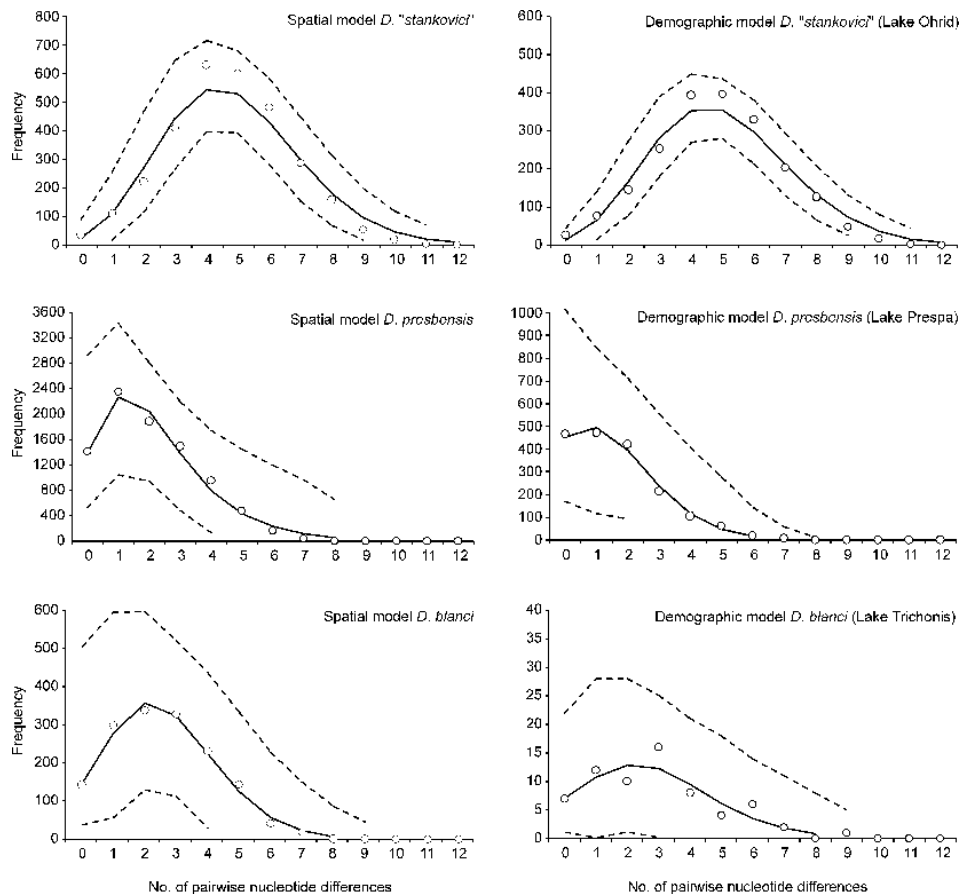


Fig. 3. Mismatch distribution of native *Dreissena* spp. based on COI mtDNA data. The distributions of pairwise nucleotide differences (circles) were tested against two expansion models (black lines): spatial expansion for all lakes (to the left) and demographic expansion out of the respective ancestral water body (to the right; see Result section for details). The 95% confidence intervals of the coalescent simulations are indicated by dashed lines.