Original Communication

The effect of altitude on distribution of freshwater algae in continental Israel

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ABSTRACT

We studied the effects of altitude, climate and hydrology on distribution of freshwater diatoms over the ecoregions of Israel. The previously recorded and recently revised taxonomic diversity of freshwater algae of Israel include 1621 species from which the diatoms constitute 32.3%. A notable feature of the taxonomic structure is a large proportion of monomorphic species with Index 1.09 ratio. Israel presents a unique diversity of algal environments from coastal plains to mountainous areas about 2000 m high and over four phytogeographic realms. Here we analyze statistical regularities of diatom distribution and compare them with the phytogeographic zonation based on higher plants. The 42 types of geographic ranges are combined in six phytogeographic domains. Five clusters of diatom taxa correspond to the coastal plains (I), the Judean and Galilean highlands (II), piedmonts (III), and the Dead Sea -Kinneret Lake Rift Valley (IV-V). Diatom flora contains both circumpolar and tropical species. The boundaries marked by the diatom distribution appear less distinct, with more numerous ecotonal species, than the corresponding terrestrial vegetation boundaries. Diatoms formed two floristic cores with centers in the Carmel and Judean mountains. The ten endemic diatoms are confined to the Rift Valley and adjacent areas of Central Negev. The differentiation of endemic species might have occurred under the impact of aridization through the Holocene and the recent warming.

Analysis shows that altitude is a major factor of diatom distribution in Israel.

KEYWORDS: diatom diversity, phytogeography, cluster analysis, altitude, distribution, Israel

1. INTRODUCTION

The effects of altitude on the freshwater algae distribution are widely discussed in the recent literature [1-6], but still remain a problem.

The previously recorded [7-8] taxonomic diversity of freshwater algae of Israel contains 1254 species of 283 genera from nine taxonomical divisions. Our investigation of last eight years encompassed all the territory of Israel and provided monitoring data for the major rivers, such as Yarqon, Qishon, Alexander, Hadera, Upper and Lower Jordan [9-18] enriching the known taxonomic diversity and revealing many new habitats. Presently, the freshwater algae of Israel include 1621 species of 289 genera from ten taxonomical divisions. In previous studies no attention has been paid to the regional distribution of algae in Israel. Therefore this paper presents the first results of our study on the effect of spatial heterogeneity in this region.

Israel presents a unique diversity of algal environments for such a small territory. The territory of Israel extends from semi-arid to arid climatic zone. Water objects mostly occur in the north and decrease to the south. The freshwater algae are collected over a wide range of altitudinal belts, from the Arava Rift Valley about 300 m below sea level and coastal plains to mountainous areas about 2000 m high and over the four phytogeo-graphic realms (Fig. 1) recognized on

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Fig. 1. Phytogeographycal realms in the Eastern Mediterranean: M- Mediterranean; I-T - Irano-Turanian; S-A - Saharo-Arabian; S - Sudanian (after [19]).

the basis of the higher plant differentiation [19]. As can be seen in the Fig. 2, the coverage of territory by studied water objects is rather dense, which gives us the basis for analyzing species diversity distribution against the terrestrial phytogeographical regions [20]. Here we analyze statistical regularities of diatom distribution and compare them with the phytogeographic zonation based on higher plants.

2. MATERIAL AND METHODS

The taxonomic and ecological information used in the following analysis is integrated in the database [21] including recent references to Israel [7-18]. The taxonomy follows the modern taxonomical system [22], which includes the recent taxonomic revision. The list also contains some taxa that are unclear in the international system.

The statistical methods are those recommended by Heywood [23] for development of floristic and taxonomic studies namely the Ward's method of percent disagreement calculation is used for constructing a similarity tree [24] of algal species diversity for the terrestrial phytogeographical regions defined by Zohary [20], and the GRAPHS program [25] for comparative floristic.

3. RESULTS AND DISCUSSION

In the first step of analysis we revealed the leading taxonomical groups of algal flora, comprising more than 50% of all species that determines the aspect of the regional algoflora. These species belong to three divisions, the Bacillariophyta, Cyanobacteria, and Chlorophyta (in order of their quantitative representation). The diatoms are the richest group of 523 species constituting 32.3% of the algal diversity. A notable feature of the taxonomic structure is a large proportion of monomorphic species represented by a single variety only.

Relationship higher/lower taxa ratio for vascular plants can characterize floristic region. Diversity



Fig. 2. Map of natural regions (ecoregions) of Israel (after [20]) showing sampling sites (black circles on insertion - sampling sites before our studies, 1878-2000; asterisk - our sampling sites 2001-2008) and clusters of statistical analysis (toned). AP - Akko Plane; AV - Arava Valley; BS - Bet Shean Valley; CC - Carmel Coast; CM - Mount Carmel; CN - Central Negev; DS - Dead Sea Area; EP - Esdraelon Plain; GC - Galilee Coast; GH - Golan Heights; GM - Gilboa Mountains; HE - Hermon; HP - Hula Plain; JD - Judean Desert; JM - Judean Mountains; LG - Lower Galilee; LJ - Lower Jordan Valley; NN - Northern Negev; PP - Philistine Plain; SA - Samaria; SH - Shefela; SN - Southern Negev; SP - Sharon Plain; UG - Upper Galilee; UJ - Upper Jordan Valley; WN - Western Negev.

ratios in Asian floras parity is more due to the temperate-tropical taxa [26]. We calculated the index of variability as ratio of infraspecies to species richness, which for the diatom algal flora of Israel is rather low, less than 1.09, which means that only few species of the total species list are divided into taxonomic varieties. It is considerably lower than in the comparable diatom floras in Europe, central-northern Asia and North America (Table 1). As can be seen, the Index of Infraspecies/Species variability in diatom floras decreased from north to south. It can be related with climate changes and can be used as criteria of future warming.

In our chorological analysis of diatom flora of Israel we recognized 42 types of species ranges combined in six phytogeographic domains. In the course of analysis, we first calculated the diatom diversity for each phytogeographical regions of Israel outlined in [20]. We then used Ward's method of percent disagreement calculation [24] for constructing a tree of similarity for phytogeographic regions diatoms diversity (Fig. 3). As a result, we revealed five clusters of diatom taxa on the level of 40% similarity corresponding to the coastal plains and the Hula Lake (I), the Judean and Galilean highlands (II), piedmonts (III), and the Dead Sea - Kinneret Lake Rift Valley (IV-V) which toned in Fig. 2.

Table 1. Variability of Index Infraspecies/SpeciesRatio in the diversity of diatom algae over theapprox latitude.

Diatom flora	Index Ratio Infraspecies/ Species	References
Poland	1.48	[27]
Great Lakes USA	1.45	[28]
Belarus	1.42	[29]
Mongolia	1.36	[30]
Central USA	1.23	[31]
Central Europe	1.21	[32-35]
British Isles	1.15	[36]
Georgia	1.19	[37-38]
Turkey	1.09	[39]
Israel	1.09	[7]



Fig. 3. Tree Diagram of five clusters (1–5) for natural regions of Israel based on statistical analysis of diatom algal species diversity by percent disagreement method; abbreviations as in Fig. 2.

The first cluster (I) comprises diatom diversity, which comes from the rivers of the coastal plain and includes also the species of the Hula Plain occurring at 140 m above - 140 m below sea level. No local endemics are found in the coastal rivers, the algal flora of which consists of widespread pollution-tolerant species. Yet in the Hula Plain we revealed two conventional endemics: *Opephora linearis* Sherm. et Patr. and *Nitzschia hulensis* Sherm. et Patr.

The Judean and Galilean highlands communities (II) constitute the second cluster. They occur at 900-1200 m above sea level and include *Cymbopleura delicatula* ssp. *judaica* Lange-Bert. et Kramm. in Nevo et Wasser, an endemic of the Upper Galilee.

The third cluster (III) includes the communities of planes and piedmonts at 50-600 m above sea level, widespread in the central and southern Israel. It includes a characteristic conventional endemic species *Gomphonema halbachii* LangeBert. et E. Reichardt in Nevo et Wasser, first found in Nahal Avedat, the Central Negev.

The Dead Sea - Arava Rift Valley communities constitute cluster (IV) representing the habitats of the bottom of rift valley at 300 m below sea level. These strongly climatically impacted communities contain Frustulia spicula ssp. judaica Lange-Bert. in Nevo et Wasser, a conventional endemic of the Dead Sea Area. Remarkably, species of Saharo-Arabian (sa) and Sudano-Sambezian (sz) phytogeographic realms Pinnularia kneuckeri Hust. Campylostylus (sa). normannianus (Grev.) Gerloff et al. (sa), Navicula massadaea Ehrlich (sa), and Amphora rognonii Gassesa (sz) are found in Israel in the Dead Sea - Arava Rift Valley only.

Cluster of the Lake Kinneret surroundings (V) includes the diatom communities occurring at 140 m below sea level as well as the Lower Jordan River outlet from the Lake Kinneret (150 m below sea level), and the Upper Jordan Valley 250 m above - 150 m below sea level. Conventional endemics are found in the Upper Jordan Valley communities alone, represented by *Stephanodiscus galileensis* Håkans. et Ehrlich, *Navicula alineae* Lange-Bert. in Nevo et Wasser, *Gomphonema ortalii* Lange-Bert. et E. Reichardt in Nevo et Wasser, *Gomphonema inkadoriae* Lange-Bert. et E. Reichardt in Nevo et Wasser, *Gomphonema alineae* Lange-Bert. et E. Reichardt in Nevo et Wasser, *Gomphonema alineae* Lange-Bert. et E. Reichardt.

The prevailing species are cosmopolitan or widespread in the Northern hemisphere, with a considerable participation of rare and endemic elements. Remarkably, the algoflora contains both circumpolar and tropical species. The species traditionally assigned to the arcto-alpine group, such as Pinnularia alpina are found in both the piedmonts and the Rift Valley, therefore being scarcely restricted to the highland habitats. As in the Mediterranean region of Dolomites Alps [1-2], Bosnia and Herzegovina [3-4], and Pyreneans [5-6], the diversity and structure of diatom communities are very closely correlated with the current velocity, which changes with altitude. Just this variable is of critical importance for distribution of the arcto-alpine group.

The group of Mediterranean species is represented not only in the corresponding terrestrial vegetation domain, but also in the Rift Valley. Yet close correspondence was found in distribution of higher plants and diatoms of the Paleotropical, Saharo-Arabian and Sudano-Zambesian provinces as defined by Takhtajan [40]. Generally, the boundaries marked by diatom distribution appear less distinct (Fig. 2), with numerous ecotonal species, than the corresponding terrestrial vegetation boundaries.

For clarifying this conclusion we used comparative floristic method [25] which has helped us with comparison of the riverine algal diversity in Israel [41]. The dendrite of taxonomic overlap (Fig. 4) shows that the diatom diversity in Israel is divided into two major groups. In first group the Carmel Mountain algal list shares species with many other floras and therefore it is placed in the center of the dendrite right core. The second core formed the Judean Mountain algal list that shares species with many other floras also (left core). Remarkable that in the right core algal diversity of the Carmel Mountain and Golan High streams, the Upper Jordan and Sharon Plain coastal rivers are closely related, whereas in left core are similar only highland communities - the Judean Mountain and the Upper Galilee streams. In the both cores the central places take the mountain diatom diversity.



Fig. 4. Dendrite of taxonomic diversity overlaps in the natural regions of Israel constructed by the similarity calculating method on the basis of Serensen-Chekanovsky indices. The floristic cores of Israeli algal diversity are marked by bold lines and outlined by dashed lines.

Therefore, analysis highlighted altitude as a major factor that influenced diatom diversity.

The endemic diatoms, altogether 10 species (about 1% of the algoflora, which is not a negligible number for a small territory), are confined to the Rift Valley and the adjacent areas of Central Negev. They are interpreted as neoendemics, reflecting the Quaternary history of the Rift Valley environments and biota and having no close relatives in the surrounding areas. This appears to be one of a few plausible examples of neodemism in diatoms.

On paleopalynological evidence [42-43] climatic conditions in the Negev were relatively humid during the Pliocene and the pluvial phases of the Quaternary, supporting vegetation of a generalized Mediterranean type. The freshwater ecosystems under such climates might have approached those of the northern Israel today [16]. Differentiation of endemic species might have occurred under the impact of aridization through the Holocene and the recent warming.

In respect of hydrochemical variables, statistical analysis of the diatom species preferences [9-17] highlighted the critical significance of salinity and organic pollution for distribution of cluster I species dominating the coastal river communities.

CONCLUSION

The previously recorded and recently revised taxonomic diversity of freshwater algae of Israel is dominated by diatoms, which contain up to 50% of species richness. A notable feature of their taxonomic structure is a large proportion of monomorphic species comparative with other diatom floras of Europe, central - northern Asia and North America. Such exceptionally low infraspecies variability might have been related to recent climatic instability and anthropogenic impacts that obliterated microhabitat differentiation and promoted highly tolerant monomorphic populations. In both the cases the Index Infraspecies/Species variability that decrease in Hemisphere from north to south can be related with climate changes and can be used as criteria of future warming.

Our statistical analysis revealed five clusters comprising the taxonomical diversity of freshwater

diatoms presently known from Israel. The clustering is primarily correlated with the altitude of habitats as a critical variable of diatom ecology. Comparative floristic method revealed two floristic cores and also highlighted altitude as a major factor that impacted of diatoms diversity distributions.

The endemic species are mostly confined to the southernmost habitats of the Negev Desert and Arava Valley as well as the Lake Kinneret. The analysis of diatom species preferences highlights species sensitive to salinity, which suggests that differentiation of endemic species might have occurred under the impact of aridization.

Remarkably, the diatom species of Arava Valley and Kinneret - Upper Jordan River are assigned to adjacent clusters of statistic analysis. Their similarity can be related to historical congruence of floristic development over the East African fault zone, to which they belong.

The relatively high endemism (ten species) in the Golan Heights - Kenneret - Dead Sea - Arava Rift Valley and adjacent areas of Central Negev is interpreted as evidence of recent speciation related to the rapid environmental changes. In particular, the narrow range species of the Dead Sea - Arava rift valley are interpreted as neoendemics, a rare case of endemism among the diatoms.

A close correspondence was found in distribution of higher plants and diatoms of the Paleotropical, Saharo-Arabian and Sudano-Zambesian provinces. As a rule, boundaries marked by diatom distribution appear less distinct, with more numerous ecotonal species, than the corresponding terrestrial vegetation boundaries.

ACKNOWLEDGEMENTS

This work was partially funded by the Israel Ministry of Absorption.

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