

Abstract

Spatial heterogeneity of biodiversity arises from evolutionary processes, constraints of environmental factors and the interaction of communities. The quality of such spatial analyses of biodiversity is improved by (i) utilizing study areas with well defined physiogeographical boundaries, (ii) limiting the impact of widespread species, and (iii) using taxa with heterogeneous distributions. These conditions are typically met by ecosystems such as oceanic islands or ancient lakes and their biota. While research on ancient lakes has contributed significantly to our understanding of evolutionary processes, statistically sound studies of spatial variation of extant biodiversity have been hampered by the frequently vast size of ancient lakes, their limited accessibility, and the lack of infrastructure around them. The small European ancient Lake Ohrid provides a rare opportunity for such a reliable spatial study. The comprehensive horizontal and vertical sampling of a species-rich taxon, the Gastropoda, presented here, revealed interesting patterns of biodiversity, which, in part, have not been shown before for other ancient lakes.

In a total of 224 locations throughout the Ohrid Basin, representatives of 68 gastropod species with 50 of them being endemic (=73.5%) could be reported. The spatial distribution of these species shows the following characteristics:

(i) within Lake Ohrid, the most frequent species are endemic taxa with a wide depth range, (ii) widespread species (i.e. those occurring throughout the Balkans or beyond) are rare and mainly occur in the upper layer of the lake, (iii) while the total number of species decreases with water depth, the share of endemics increases, (iv) the deeper layers of Lake Ohrid appear to have a higher spatial homogeneity of biodiversity and related environmental factors, (v) biotic interaction due to possible spillover effects may contribute to the establishment of hotspots, and (vi) eco-insularity within the Ohrid Basin occurs at two levels, at the level of the lake proper and at the level of the feeder-springs.

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

It is also shown that large scale effects such as type of water body or water depth are mainly responsible for the distribution of biodiversity. In addition, small scale effects like environmental gradients or biotic interaction affect gastropod composition within a particular depth zone.

1 Introduction

Biodiversity, the variation among living organisms or ecosystems (UNEP, 1992), is known to be heterogeneous in temporal (e.g., Rohde and Muller, 2005; Weir, 2006) and spatial distribution (e.g., Diniz-Filho and Bini, 2005; Buckley and Jetz, 2008). Spatial variation of biodiversity, in general, is thought to be shaped by large scale factors such as latitudinal gradient, altitude or water depth, and peninsula or bay effects. Factors acting on smaller scales include habitat heterogeneity, barriers to dispersal, predation, competition or mutual stimulation (Gaston and Spicer, 2005). The prevailing state of these factors influences biodiversity patterns, but temporal dynamics are likewise important (Gaston, 2000). Several biodiversity measures have been proposed (Purvis and Hector, 2000) to account for biodiversity, though species richness (alpha diversity, Whittaker, 1972) is considered to be a good, easily accessible and intuitive proxy for ecological, genetic and organism diversity (Gaston, 2000; Vellend, 2005).

Unfortunately, our knowledge of biodiversity patterns is strongly biased towards marine or terrestrial habitats (Gaston and Spicer, 2005) and to conspicuous taxa like vertebrates (e.g., Abell et al., 2006; Strayer, 2006). Thus, our level of understanding of patterns in freshwater invertebrate distribution remains limited, raising the need for comprehensive studies (Hof et al., 2008).

To enable a spatial analysis of freshwater biodiversity some prerequisites should be fulfilled: (i) ideally the area studied should be well defined based on natural entities rather than geopolitical ones, (ii) the majority of the studied taxa should occur exclusively in the study area to reduce the impact of widespread species on biodiversity estimates and to avoid scaling problems (Gaston, 1997), and (iii) the taxon of inter-

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



est should be characterized by high biodiversity and in-homogenous distribution, to diminish the correlation between local and regional diversity relationships (Gaston and Spicer, 2005).

The first prerequisite is typically met by ancient lakes, that is, water bodies that have continuously existed for at least hundred thousand years. They often show a high degree of biodiversity, and so they have attracted numerous studies of both fossil (Williamson, 1981; but see Van Boxclaer et al., 2008; Harzhauser and Mandic, 2008) and extant lake biota (Wilson et al., 2004; Herder et al., 2006). Cohen (1994) emphasized that the species richness we see in ancient lakes today could be a temporary snapshot. Lake-level fluctuations and changes of basin morphology with considerable effects on lake biota, for example, are well documented for ancient lakes of the East African Rift Valley (e.g., Cohen et al., 2007; Scholz et al., 2007; Schultheiß et al., 2009), Lake Baikal (Kashiwaya et al., 2001), or the Caspian Sea (Reid and Orlova, 2002; Grigorovich et al., 2003). Comparable data about hydrological changes in the European ancient Lake Ohrid have been published only recently (Belmecheri et al., 2009; Lindhorst et al., 2010).

Lake Ohrid is a graben lake of bathtub shape with a maximum depth of 289 m, a surface area of 358 km² and a volume of 55 km³ (Matzinger, 2006a). Hence, it is one of the smallest ancient lakes of the world. Nevertheless, the Ohrid Basin has a complex geological and limnological structure. Different bedrock types, active tectonics (for details see Hoffmann et al., 2010), steep-sided mountain ranges and water-discharge by lake-side and sublacustrine springs (Matzinger, 2006b) cause the characteristics of different habitats (Fig. 1). Some workers have suggested that these complex features are partly responsible for a high number of ecological niches and an outstanding degree of biodiversity (Radoman, 1985; Albrecht and Wilke, 2008). Moreover, due to an exceptionally high degree of endemism, Lake Ohrid is quite distinct from other Balkan lake systems (Albrecht et al., 2009; Marková et al., 2010; Trajanovski et al., 2010).

While Lake Ohrid, indeed, appears to have a fairly isolated basin, thus fulfilling criterion (i) for spatial analysis of freshwater biodiversity, criteria (ii) and (iii), addressing

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

requirements of the taxon to be studied, are met by representatives of its gastropod fauna.

Compared to some other ancient lakes, the vast majority of Lake Ohrid's gastropod species is morphologically relatively easy to distinguish and gastropods probably constitute the best studied invertebrate taxon in the lake (e.g., Poliński, 1929; Hubendick and Radoman, 1959; Radoman, 1985; Hauswald et al., 2008; Wilke et al., 2009). Recently, even the first fossil molluscs have been reported from the Last Interglacial period (Albrecht et al., 2010). Moreover, there is growing evidence for vertical and horizontal gradients and barriers within the Ohrid Basin (Albrecht et al., 2006, 2008; Wysocka et al., 2008; Trajanovski et al., 2010), possibly promoting parapatric or even allopatric speciation events (Albrecht and Wilke, 2008). Despite these interesting findings, a comprehensive picture of the spatial distribution of gastropod biodiversity within Lake Ohrid is still missing. However, this is not a problem typical for Lake Ohrid. In fact, we have no knowledge of any ancient lake in the world where a species-rich invertebrate taxon has been sampled in a manner allowing for statistically sound studies of the spatial distribution of biodiversity. Reasons include the often large size of ancient lakes, their, in part, limited accessibility (both physically and politically), and the lack of infrastructure for lake-wide biodiversity studies.

In this regard, Lake Ohrid constitutes a rare exception. Not only does the relatively small size of the lake allow for comprehensive sampling but the lake is also readily accessible, and infrastructure for lake-wide biodiversity studies can be regarded as excellent. Given this unique opportunity for a comprehensive horizontal and vertical sampling of a species-rich taxon over a whole ancient lake basin, we are using information from 224 collecting points for gastropods from Lake Ohrid to:

- (i) provide the first comprehensive assessment of Lake Ohrid's gastropod diversity,
- (ii) identify potential faunal subdivisions of the Ohrid Basin utilizing a multivariate framework, and

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

(iii) provide a spatially-explicit description of biodiversity patterns within the lake proper.

2 Material and methods

2.1 Zonation of the Ohrid Basin

5 The basin of Lake Ohrid, that is, the intersection between paleoshorelines (N. Hoffmann, personal communication, 2010) and the conjunct surface watershed, has a size of 1605 km² (Fig. 1). It consists of the lake itself as well as surrounding lotic waters, pools, and springs.

2.1.1 Lake Ohrid

10 The vertical subdivision of worldwide lakes is typically reflected by the degree of benthic photic production with the littoral being the zone of macrophytic vegetation and the profundal being the layer without photic production. In deep oligotrophic lakes such as Lake Ohrid, it is difficult to infer an exact zonation based on biotic factors. Thus, we here adopted a strictly hydrological approach based on lake-level fluctuations and the
15 location of the summer thermocline.

Surface Layer

The Surface Layer is the upper vertical zone in Lake Ohrid down to approximately 5 m depth. It is affected by wave action of up to 1.5 m height (Stanković, 1960), moderate intra-annual lake-level fluctuations of 1 m (Popovska and Bonacci, 2007), and
20 high seasonal temperature variations (Stanković, 1960). The vegetation of the Surface Layer consists mostly of microalgae and extensive reed belts at the northern and southern shores (Watzin, 2002). Based on prevailing abiotic conditions, such as sub-lacustrine springs, substrate type and differences in geology (Hoffmann et al., 2010),

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



a specific horizontal zonation of the Surface Layer has been suggested (Albrecht and Wilke, 2008).

Intermediate Layer

The Intermediate Layer is summer stratified by a relatively steep temperature decline and increase of dissolved oxygen. It consists of a partly continuous (Lindhorst et al., 2010) belt of *Chara* algae between 3–20 m water depth, which impedes the migration of benthic invertebrates (Albrecht et al., 2006; Sell et al., 2007; Wysocka et al., 2008). The shell zone below the *Chara*-belt is characterized by broad *Dreissena* beds (e.g., Wilke et al., 2010) and by sparse macrophytes (Stanković, 1960).

Deep Layer

The upper boundary of the Deep Layer is characterized by the end of the summer thermocline at ~25 m (Watzin, 2002) and higher oxygen saturation than upper zones (Stanković, 1960). As the first zone of definite fine-grained sediment deposition (Stanković, 1960), the substratum consists mainly of silt and mud (Vogel et al., 2010), and sporadic oxygen-depletion influences organic matter preservation (Holtvoeth et al., 2010). Below the 50 m isobath to the bottom of Lake Ohrid, there is no benthic photic production (Stanković, 1960).

2.1.2 Springs

Springs represent an important hydrological system in the Ohrid Basin as they are responsible for a considerable part of its water balance. They can be found within the lake (i.e. sublacustrine) or along the margins. The majority of them are located in the northwest and northeast of the lake, but the most powerful springs are the feeder spring complexes of Sv. Naum (Macedonia) and Tushemisht/Zagorican (Albania) in the south. They form spring lakes of up to 5 m depth (Kunz, 2006). Mainly supplied

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



by neighbouring Lake Prespa, the feeder-springs are characterized by different water chemistry than the mainly precipitation-fed springs in the northeast and northwest (Matzinger, 2006b). Thus, we here distinguish between two different types of spring: The southern feeder-springs and the northeastern/northwestern springs.

2.1.3 Lotic waters and pools

Many of the northeastern and northwestern springs give rise to creeks and small, often artificial pools. Due to the steep-sided basin shape, the lotic waters are mainly short, shallow and often subject to seasonal desiccations. The two main lotic waters in the area are the effluent Crni Drim River and the affluent Sateska River (Fig. 1). The latter was artificially diverted into the lake in 1962 (Matzinger et al., 2006a).

2.2 Sampling gastropod fauna

Gastropods from the Ohrid Basin were collected during seven field trips carried out between May 2003 and September 2009. Individuals were obtained by hand collecting from hard substrata in shallow waters or from stones and rocks lifted when snorkelling. Soft substratum and plant material was sieved. Deeper parts of Lake Ohrid down to 60 m were sampled using a triangular dredge from small boats or from the Hydrobiological Institute Ohrid (HBI) research vessel. Data on sampling locations were recorded with a GPS device and stored in a database. Equal distance measurement for longitude and latitude degrees was obtained by transforming coordinates to UTM projection.

All materials are deposited at the permanent DNA, shell and tissue collection of the University of Giessen, Systematics and Biodiversity Group (UGSB). Species determination and nomenclature for gastropod samples follows Poliński (1929), Hubendick and Radoman (1959), Radoman (1983), Bodon et al. (2001), and Albrecht et al. (2006, 2008). A total of 284 samples were obtained during field work. Because of multiple collections at selected sites, 284 collecting events resulted in a total of 224 analysed collecting points. Non-parametric Wilcoxon tests showed no significant difference of species

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



richness data between the pooled and unpooled datasets (Surface Layer: $W=5210$, $P=0.077$; northeastern and northwestern springs: $W=205.5$, $P=0.2446$; lotic waters: $W=182.5$, $P=0.9149$; feeder springs: $W=1153$, $P=0.4828$).

We calculated the normalized endemic species (N) area (A) index according to Eq. (1) (modified after Albrecht and Wilke, 2008).

$$I = \frac{\lg(N + 1)}{\lg(A + 1)} \quad (1)$$

2.3 Statistical analysis

2.3.1 Community composition and species richness

The number of species, proportion of endemics and species frequencies are important characteristics of ecosystems and local subdivisions, and may give clues as to the underlying abiotic constraints and/or different evolutionary histories (Cooper and Purvis, 2010).

First, species collecting frequencies were estimated and species were classified into rare, common and frequent. We used the rarefaction method for each species at each depth layer, because of unbalanced collecting frequencies in the three different depth zones. Species frequency and standard deviation was obtained for the lowest number of collecting points ($N=34$, Deep Layer) by random site accumulation of one layer with 4999 permutations. Calculation was performed with the vegan package (Oksanen et al., 2010) for the R statistic environment (R Core Development Core Team, 2009).

To test for faunal subdivision of the different layers within the Ohrid Basin, we compared gastropod community compositions. Species composition within a layer should be more similar than that of communities from different layers. Our hypothesis of distinct gastropod communities based on presence/absence data and Bray-Curtis dissimilarities was tested by a one-factorial, permutational analysis of variance (PERMANOVA, Anderson, 2001) utilizing the function `adonis` of the vegan package with

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



4999 permutations. For explorative data analysis, we used non-metric multidimensional scaling (NMDS) to transform similarity of species composition into an illustratable low-dimensional figure. The applied vegan function metaMDS was stopped when two convergent ordinations with highest goodness-of-fit compared to original data structure were reached. The number of dimensions was selected in line with the suggestions of Kruskal and Wish (1978). 1000 null models were generated with the trial swap algorithm (Miklos and Podani, 2004), to check whether a better ordination structure could be achieved by chance. This technique preserves species richness per collecting point and species occurrence frequency. Water depth and species richness of the collecting points were fitted to the ordination of the lake proper and statistical testing was achieved by 4999 permutations.

Differences in mean species richness of distinct layers were tested by a one-factorial PERMANOVA with 4999 permutations.

2.3.2 Analyses of spatial patterns

In contrast to large scale differences in biodiversity, that is, between different zones of the Ohrid Basin, fine scale variations within a layer are more difficult to disentangle because of possibly co-varying environmental factors. This hampers, factor based a-priori classification and subsequent testing. However, spatial autocorrelation of environmental factors is likely (Legendre, 1993) and should be reflected by similar observations on species richness from nearby collecting points. An increasing number of studies benefits from straightforward eigenvector-based filters of, for example, phylogenetic information (Kühn et al., 2009) or, as initially suggested, small scale descriptors of spatial autocorrelation (Borcard and Legendre, 2002). A great advantage of these spatial filters, commonly called principal coordinates of neighbouring matrices (PCNM), is that they avoid grid based methods, in which a-priori selected grid sizes frequently influence results (Gaston and Spicer, 2005). As grid data often originate from merged sampling points, techniques that focus on analysing point patterns and associated processes are established (e.g., Ripley, 1977; Wiegand and Moloney, 2004). They enable, for

example, the detection of global spatial clustering or biotic interactions, like inhibition or mutual stimulation.

First, horizontal and vertical variations of species richness in Lake Ohrid were compared utilizing a heat map generated by the R package spatstat 1.17-5 (Baddeley and Turner, 2005). Three ESRI shapefiles (ESRI, 2008) were imported into R, because of the identification of at least three bathymetrically different layers (see above, Albrecht and Wilke, 2008), using the package maptools 0.7-29 (Lewin-Koh and Bivand, 2009). All collecting points were allocated to the appropriate bathymetric layer. The function smooth.ppp was applied, to mitigate unequal point distribution with a Gaussian kernel weighting of a radius of 2 km. The 156 collecting points of the lake proper were marked with their alpha diversity. Species richness between two collecting points was estimated using a Gaussian smoothing factor.

For spatially explicit description of small scale differences in biodiversity we here used PCNMs. Accordingly, spatial predictors of alpha diversity for the whole lake proper, Surface Layer, intermediate layer and Deep Layer were created. This approach computes a diagonalized matrix of Euclidean distances for the point coordinates by truncating all pairwise distances above a fourfold threshold value (Borcard and Legendre, 2002). In the four tested scenarios, the values of 3868 m, 4749 m, 6746 m and 8152 m were the longest pairwise distances between two points in a minimum spanning tree based on principal coordinate analyses (PCoA) of eastings and westings. Thus, all collecting points above this threshold value were not considered as neighbours and were allowed to receive different species richness values in consecutive simulations. If a significant correlation between species richness and spatial distance was detected by a linear regression (Borcard and Legendre, 2002), diversity data were detrended by weighting them with their residuals. The vegan function pcnm (Oksanen et al., 2010) was used to construct those eigenvectors with positive eigenvalues for the lake proper and every bathymetric layer. According to Blanchet et al. (2008), a global test for significance was obtained with all PCNMs using the permutest function with 4999 permutations. If a p-value was lower then 0.05, the forward selection function with 4999

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



permutations of the packfor package (Blanchet, 2009) for non-normal distributed data was used to obtain significant spatial descriptors.

To test our null hypothesis of independent relationships between species richness values at different locations, mark correlation functions (MCF) of the different vertical layers of the lake proper were computed, based on species richness values. The function markcorr of the spatstat package calculates the dependence $pf(r)$ between the values of two points at a given distance r (Stoyan and Stoyan, 1995). A value of 1 indicates no correlation, values higher than 1 suggests mutual stimulation and values lower than 1 suggest inhibition. The method sm was applied to create a balance for unequal point distances using non-parametric kernel density estimation. The null hypothesis was rejected in cases exceeding the 95% confidence envelopes generated by Monte-Carlo simulations of 99 null models (5th highest and 5th lowest value; Wiegand and Moloney, 2004).

3 Results

3.1 Taxonomic distribution and endemism

A total of 68 gastropod species was found in the Ohrid Basin, with 50 of them (73.5%) being endemic. Calculating the normalized endemic species area index with an area of 1605 km² gave 0.532. Following the species based rarefaction of the lake species (Fig. 2), we applied the criterion of Williams et al. (1996). Those species that account for the top 20% quantile were considered to be frequent species and the same proportion at the lower tail as rare. Frequent species were found at up to one third of all sampling points. The majority of species was found at 1–12% of all sampling locations and was regarded to be common. The 11 rare species could only be found at less than 1% of all sites and most of them were non-endemics. No gastropod specimens were found in high mountain springs and below 60 m water depth.

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



3.2 Community composition and species richness

Explorative analyses of gastropod community similarities showed differences between the zones of the Ohrid Basin (Fig. 3a) as well as within Lake Ohrid (Fig. 3b). The two-dimensional ordination of the whole basin reached two convergent solutions after 1070 runs and revealed a Kruskal stress value of 19.39, indicating marginal congruence with the original data structure. However, none of the 1000 null model species communities attained a lower value. A partitioning into Lake Ohrid, feeder springs, lotic waters and northeastern/northwestern springs was supported by a significant zonation effect on community composition ($F_{3,220}=21.48$, $P<0.001$). The three-dimensional NMDS of the Lake Ohrid communities converged after 16 runs and had a stress value of 15.4. Vector fitting showed a highly significant correlation between ordination structure and collecting depth ($R^2=0.79$, $P<0.001$) as well as species richness ($R^2=0.48$, $P<0.001$). Again, no superior ordination could be achieved by any of the null models. The differences between species assemblages in the three lake layers were also supported by a significant PERMANOVA result ($F_{2,153}=29.18$, $P<0.001$).

The different layers are characterized by different numbers of widespread, endemic and layer endemic gastropod species (Fig. 4a). The three different layers of Lake Ohrid harbour more species and endemics than outside water bodies. However, the northeastern and northwestern springs as well as the feeder-springs revealed the highest proportion of point endemic species.

Alpha diversity (Fig. 4b) differed between layers of the Ohrid Basin ($F_{3,220}=15.68$, $P<0.001$) as well as within Lake Ohrid ($F_{2,153}=19.73$, $P<0.001$). The Intermediate Layer showed the highest alpha diversity with a mean of 8.8 ± 1.4 gastropods per collecting point, whereas the lotic waters and northern springs harboured the lowest number of species (2.5 ± 0.6 ; 3.0 ± 0.8).

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

3.3 Spatial analysis

Species richness maps (Fig. 4c,d) showed a relatively homogeneous distribution of gastropod species in the deep and Intermediate Layer whilst the highest variation occurred in the Surface Layer.

5 Acknowledging that we did not apply a statistical model for identifying places with elevated degrees of endemic biodiversity (“hotspots” sensu Prendergast et al., 1993), candidate places as shown in Fig. 4d are the area around Veli Dab (southeastern shore) of the Surface Layer as well as areas of the Intermediate Layer off Sv. Naum (southern shore) and off Hudenisht (southwestern shore).

10 After detrending, the Surface Layer was the only zone which passed the global test ($P < 0.05$) of significant explanatory power of all PCNMs for alpha diversity. In detail 88, 20 and 22 spatial descriptors were constructed for the whole lake proper, the Deep Layer and the Intermediate Layer, but could not significantly explain the observed species richness patterns of those entities. For the Surface Layer, forward selection of significant ($P < 0.05$) eigenvectors out of the 49 constructed ones resulted in a choice of six PCNMs (Fig. 5) with a cumulative adjusted R^2 of 0.4. It was not possible to tag the exact spatial scale of single PCNMs, because of the unequal distances between the sampling points. But PCNMs with low indices are spatial filters at larger distances, whereas consecutively higher indices describe similarity of species richness on smaller scales. Hence, five out of the six selected PCNMs are considered to describe large scale variation of alpha diversity in the surface layer. The linear trend ($P < 0.05$) previously removed explained 4.5% of the species richness by coordinates.

25 A MCF (Fig. 6) based on distances between sampling points and alpha diversity showed no dependence for the Deep Layer. The function of the surface- and Intermediate Layer exceeded the upper and lower interval of critical values of no correlation, respectively. This indicates species richness above and below the expectations merely by location of the sampling point.

4 Discussion

Our results suggest the existence of distinct gastropod communities in the different zones of the Ohrid Basin. The rivers and northeastern and northwestern springs are species poor, the southern feeder-springs show moderate mean species richness, and all zones of the lake proper are species rich, except for the Deep Layer. However, all three depth zones are almost exclusively inhabited by endemics. The intermediate layer has the highest mean alpha diversity. The Surface Layer shows the highest variation of alpha diversity and features Lake Ohrids' candidate hotspot for species richness at the southeastern shore. Species richness seems to correlate to the spatial distribution of environmental factors of this uppermost lake layer is suggested.

4.1 Endemism and species frequency

The total number of 68 gastropod species and the total number of 50 endemic species found in our study are only slightly lower than those reported in Radoman (1985), that is, 72 and 56 species, respectively. It should be noted, that the numbers published by Radoman are based on approximately 30 years of field work. The six endemic species not rediscovered in our recent sampling are known to have been described from empty shells, are only sporadically released from subterranean springs, or are rare Deep Layer species. Accordingly, the rate of endemism (73.5%) is also lower than the 78% suggested by Radoman (1985). In addition, we collected three widespread species previously unknown to the Ohrid Basin, which further reduces the rate of endemism. On the other hand, recent molecular studies (Albrecht et al., 2006, 2008) revealed the existence of two new cryptic feeder spring species. Albrecht and Wilke (2008) emphasized the lack of knowledge concerning the evolutionary history of many taxa and that future molecular studies will probably result in the discovery of more new endemic species in Lake Ohrid (also see Schultheiß et al., 2008 for a molecular study on pea-clams and Marková et al., 2010 for cryptic phylogenetic subdivision in a cyprinid species). Lake Ohrid is only outnumbered by the ancient lakes Baikal, Tanganyika and

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the Malili lakes in terms of the total number of endemic gastropod species. However, taking surface area into account by applying the normalized endemic species area index (Albrecht and Wilke, 2008), Lake Ohrid surpasses other ancient lakes in terms of endemic gastropod biodiversity (Albrecht et al., 2009).

5 In Lake Ohrid, a high proportion of gastropod species are endemics (Fig. 4a), many of them common (Fig. 2) and relatively unconfined regarding their depth preferences. Interestingly, the rare species are almost exclusively non-endemics and occur mostly in the surface layer. In fact, there appears to be a positive correlation between species frequency and depth range.

10 An obvious shift in the frequency of endemic species occurrences at sites could not be detected, compared to previous reports (e.g., Hadžišče, 1956; Stanković, 1960; Radoman, 1983).

However, an increasing number of widespread species are observed living in areas of the highest anthropogenic pressure in the southwestern (Lin Peninsula) and north-eastern (Ohrid Bay, Sateska estuary) parts of the lake (Fig. 4d, also see Kostoski et al., 2010).

Moreover, a shift in species depth range appears to be possible. Whereas we were unable to find specimens below depths of 60 m, occurrences at up to 100 m depth were reported by Radoman (1985).

20 4.2 Faunal subdivision of the Ohrid Basin

Little faunal overlap was observed in the ordinations shown in Fig. 3. Hence, our results suggest, on the one hand, a good separation of lake gastropod communities from the surrounding watershed, whilst on the other hand, a fair degree of separation among communities of feeder springs versus northwestern/northeastern springs and lotic waters (Fig. 3a) is also shown.

25 In addition, there are distinct differences among the three depth layers of the lake itself (Fig. 3b) with significantly different alpha diversities. The Intermediate Layer showed the highest number of species per collecting point, but also the lowest num-

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

ber of species exclusively restricted to a single depth layer. Whereas annual water level fluctuation and wave action restrict plant and bacteria growth in the Surface Layer (Stanković, 1960), the Intermediate Layer is relatively undisturbed, yet enough light reaches this layer (Stanković, 1960). Therefore, this photic zone is known to be the most bio-productive layer in Lake Ohrid (Tocko and Sapkarev, 1978). Similar patterns of elevated species richness in intermediate layers were observed in ancient lakes Tanganyika (Michel, 1994), Baikal (Sitnikova, 2006) and Titicaca (Dejoux, 1992). In contrast, the Caspian Sea shows a rather continuous decline of species richness and density with increasing water depth (Parr et al., 2007). However, elevated species richness in shallow parts is suggested to be a general feature of ancient lakes (Martens, 1997). No comprehensive species richness study of other taxa has been conducted in Lake Ohrid so far. But abundance data for e.g., phytoplankton or chironomids suggest a similar peak value at the Intermediate Layer, whereas Oligochaeta, Amphipoda and especially Ostracoda showed their highest densities in deeper waters (Stanković, 1960; Mikulic and Pljajic, 1970).

As proposed by Boss (1978), a common feature of ancient lakes is eco-insularity. Accordingly, well adapted ancient lake organisms may out-compete most invading species but are probably inferior outside the native lake. Hence, little faunal overlap is expected in the case of eco-insularity. The recent lake shore, however, may not necessarily constitute the “island” border. There are examples showing endemics range limits corresponding to the watershed border (Glaubrecht and Rintelen, 2008; Schultheiß et al., 2009). In Lake Ohrid, the situation appears to be more complex. Whilst we do see eco-insularity on a basin scale (Albrecht et al., 2009), we also see evidence for two patterns within the basin: eco-insularity of the lake proper and eco-insularity of the feeder-springs.

Interestingly, the species richness map (Fig. 4c) shows relatively uniform distributions of alpha diversity for the Deep Layer and Intermediate Layer. The Surface Layer, however, is characterized by a rather heterogeneous species richness distribution, with a hotspot inferred at the rocky southeastern shore (see below). The spatial descriptors

inferred in our modelling of species richness variation of the Surface Layer (Fig. 5) are likely caused by co-varying environmental factors (sensu Borcard et al., 2002).

Indeed, spatial gradients of sediment features are shown (Vogel et al., 2010) and different substrata is likely to affect species distribution and biodiversity (Kershner and Lodge, 1990; Michel, 1994).

4.3 Hotspots of biodiversity

Of the three suggested biodiversity hotspots, the area around Veli Dab, appears to be outstanding in terms of point endemism. This hotspot, comprising an area of less than 1 km², harbours >10% of Lake Ohrids' endemic gastropod biodiversity (Fig. 4a; also see Wilke and Albrecht, 2007). This is largely due to the fact that all point endemics of the Surface Layer were exclusively found in this particular area. These taxa are known to require a specific environment the so-called "littoral interlithon", that is, a patchy system of porous stones or rocks often associated with sublacustrine springs (e.g., Hadžišče, 1956; Albrecht and Wilke, 2008).

Interestingly, an increasing number of widespread species are observed living in areas of the highest anthropogenic pressure in the southwestern (Lin Peninsula) and northeastern (Ohrid Bay, Sateska estuary) parts of the lake (Fig. 4d, also see Kostoski et al., 2010b).

One of the most surprising findings of our study, however, is the presence of mutual stimulation as indicated by the mark correlation study (Fig. 6). It clearly shows that alpha diversity at single points benefits from surrounding species richnesses. A spillover effect is likely, that is, the dispersal of specimens from the species' range centres to more marginal parts.

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



5 Conclusions

This spatially comprehensive study of a large taxon revealed interesting patterns of biodiversity in the Ohrid Basin. The total number of 68 species of gastropods here reported with 73.5% of which are endemic does not substantially differ from the numbers generated decades ago. We also did not find significant differences in the frequency of species occurrences at sites. We do, however, see a moderate trend indicating a decrease in endemic species and an increase of widespread species.

Little faunal overlap was observed in the NMDS analysis, indicating strong effects of eco-insularity for the Ohrid Basin. Moreover eco-insularity appears to act on two spatial scales – the lake proper and the feeder springs.

Variation of community assemblages and species richness is likely to be explained by hierarchically structured effects acting on different scales. Large scale effects such as type of water body and lake depth do, indeed, cause broad differences, while small scale effects like environmental gradients or biotic interactions typically cause minor differences in biodiversity distributions on a smaller spatial scale. However, one of these biotic interactions – mutual stimulation – may play a larger role in explaining species richnesses than has previously been thought.

Alpha diversities of the Deep and Intermediate Layers show relatively uniform distributions. In contrast, only the Surface Layer is characterized by a heterogeneous species richness distribution. This species richness variation is likely caused by co-varying environmental factors.

Interestingly, many endemic species are very common (Fig. 2) and relatively unconfined regarding their depth preferences. In contrast, non-endemic species are mostly rare species, typically being restricted to limited areas of the Surface Layer.

All point endemics of the lake proper reported in our study are to be found in a single biodiversity hotspot at the rocky southeastern shore. This site thus harbours >10% of Lake Ohrids' endemic gastropod biodiversity.

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

While our study shows a strong correlation between the spatial distribution of gastropod biodiversity and hydrological features of ancient lake Ohrid, future studies should focus on disentangling the relationship of community distributions and environmental factors which affect habitats.

5 *Acknowledgements.* We are grateful to our colleagues at the Hydrobiological Institute Ohrid for their valuable support. D. Georgiev (Ohrid) supported our field work with his immense local expertise. Sincere thanks are given to all student colleagues for making the field work a pleasant experience and S. Nachtigall for assistance in the laboratory. This research was supported by DFG grants to TW (WI 1902/8-1) and CA (AL 1076/3-1).

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BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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5

BGD

7, 4953–4985, 2010

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



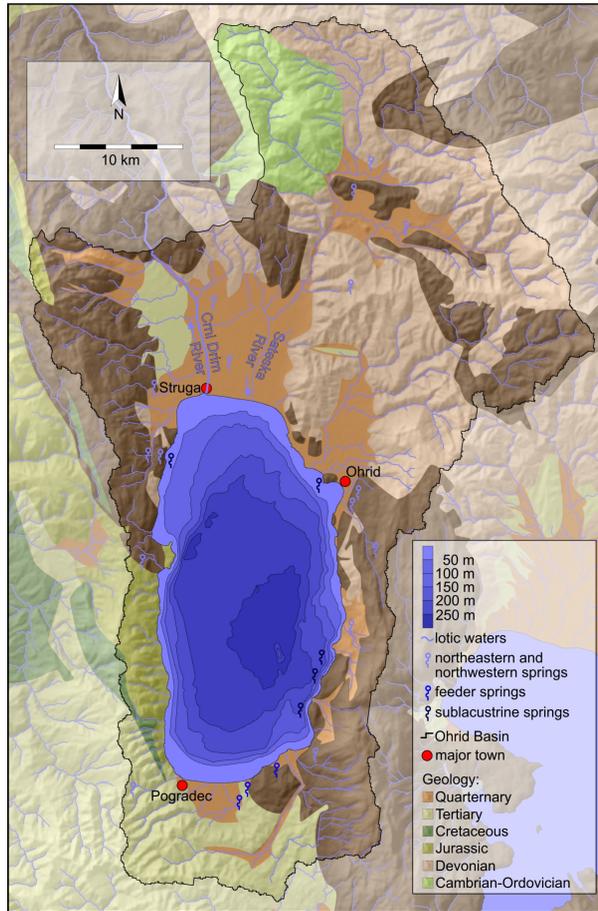


Fig. 1. Map of the Ohrid Basin indicating major hydrological and geological features. Map adapted from Hoffmann et al. (2010).

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page	
Abstract	Introduction
Conclusions	References
Tables	Figures
◀	▶
◀	▶
Back	Close
Full Screen / Esc	
Printer-friendly Version	
Interactive Discussion	



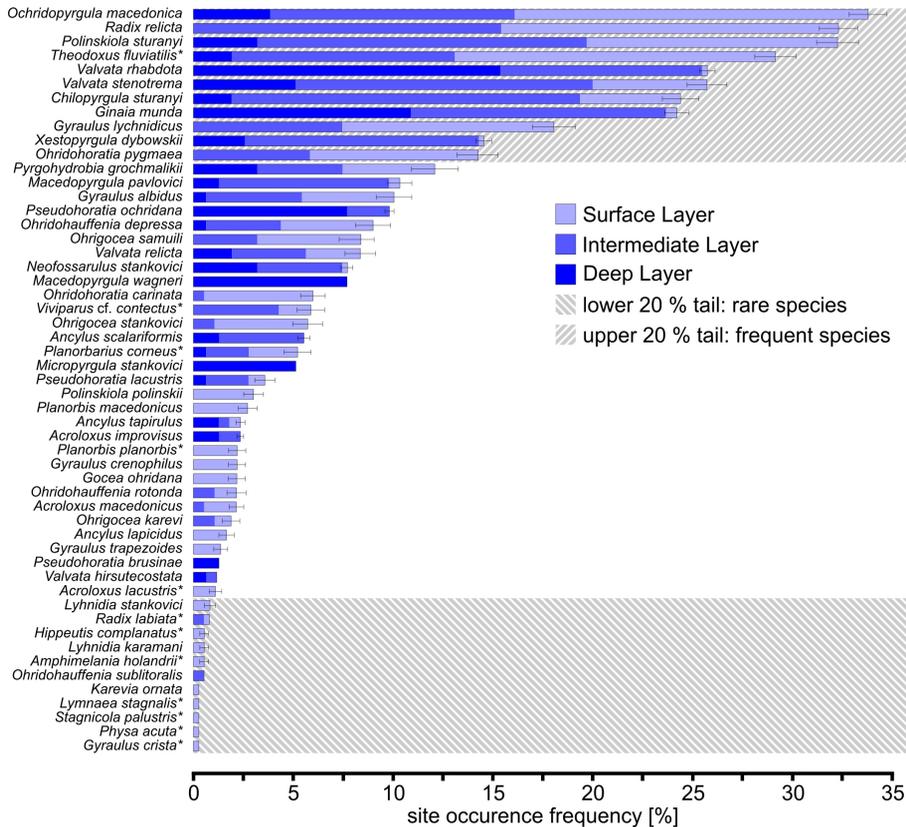


Fig. 2. Plot of frequency and standard deviation of species sites occurrence of gastropod species found in Lake Ohrid. Depth layers are colour-coded and non-endemic species are marked by asterisks.

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

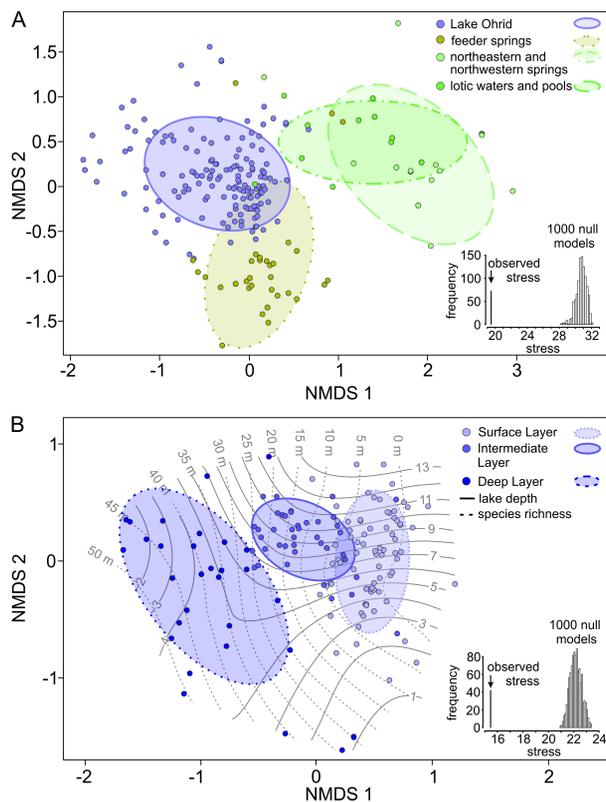


Fig. 3. NMDS plots of gastropod communities (Bray-Curtis dissimilarity). **(A)** Two-dimensional solution within the Ohrid Basin. **(B)** Vector fitting of sampling depth and species richness for three-dimensional solution within Lake Ohrid.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

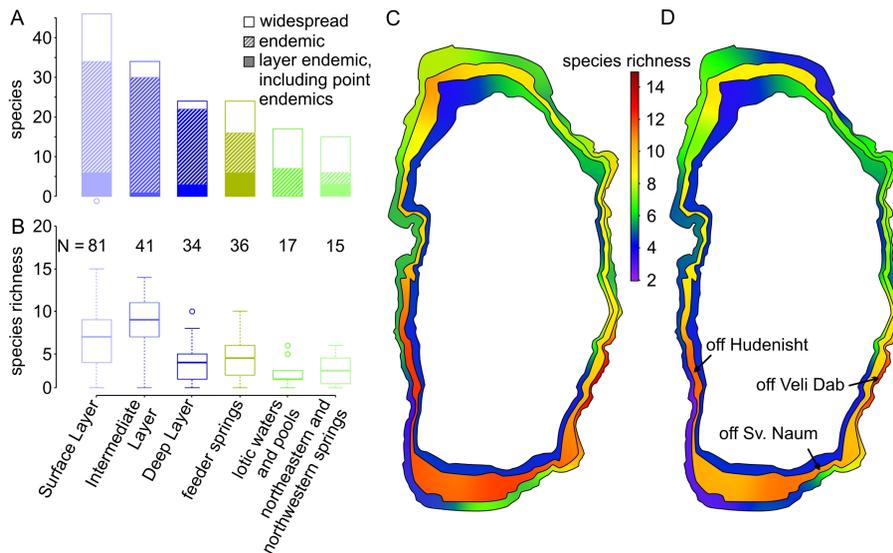


Fig. 4. Zonation-specific analyses of gastropod species richnesses in the Ohrid Basin. **(A)** Bar plots of species compositions. **(B)** Quartile box plots of species richness including median, upper and lower quartiles (boxes) and 1.5 interquartile range whiskers. **(C)** Species richness map based on all species. **(D)** Species richness map based on endemics. Candidate hotspots of endemic species richness are indicated by arrows. Because of the strong slope at the eastern and western tectonic faults, the depth layers could have a width of less than 10 m, and were thus stretched to ensure proper resolution.

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

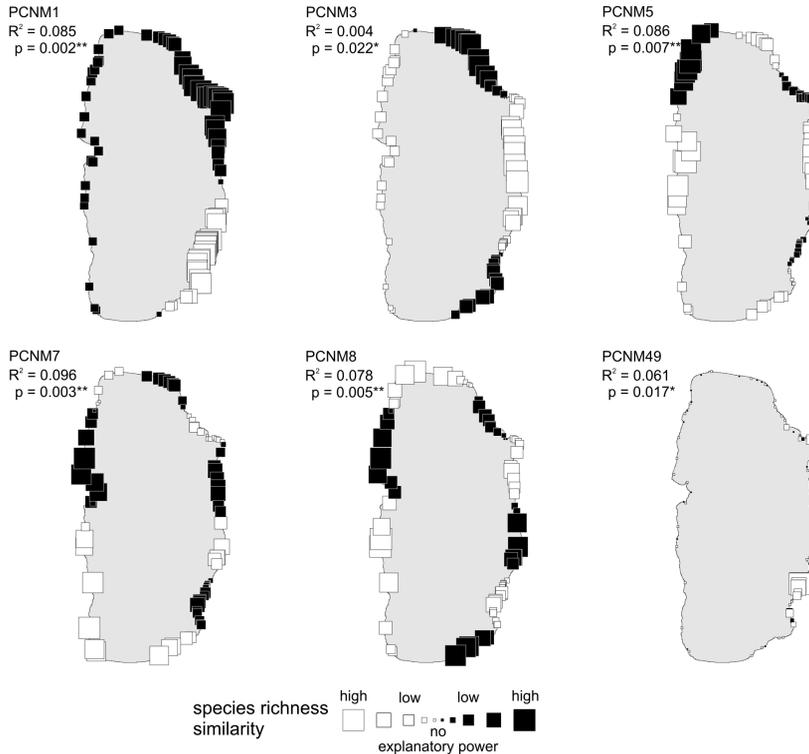


Fig. 5. Plot of PCNM eigenfunctions estimating gastropod species richness similarities within the Surface Layer of Lake Ohrid. Five broad and one fine scale vectors explain 40% of the spatial variation of alpha diversity. Within each eigenfunction, groups of equally-coloured squares indicate similar species richnesses. Increasing square size shows higher similarity in alpha diversity (note that small squares may not have sufficient explanatory power). Note that higher eigenfunctions represent increasingly smaller spatial scale predictions. Therefore, the frequency of alternating groups of black and white squares increases.

Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatially explicit analyses of gastropod biodiversity

T. Hauffe et al.

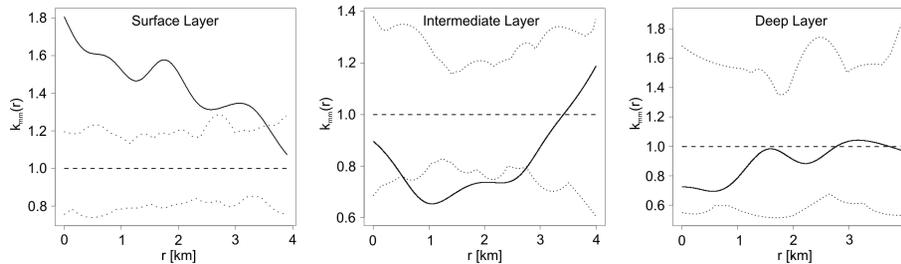


Fig. 6. Plots of mark correlation function (solid line) for the relationship between gastropod species richness and the distance between sampling locations within different layers of Lake Ohrid. No correlation is indicated by the horizontal dashed lines, the 95% confidence envelope by dotted lines. Values above and below the confidence envelope indicate mutual stimulation or inhibition, respectively.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion