

Assembly processes of gastropod communities change with horizontal and vertical zonation in ancient Lake Ohrid: A metacommunity speciation perspective

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Abstract. The Balkan Lake Ohrid is the oldest and most diverse freshwater lacustrine system in Europe. However, it remains unclear whether species community composition and the diversification of its endemic taxa is mainly driven by dispersal limitation, environmental filtering, or species interaction. This calls for a holistic perspective involving both evolutionary processes and ecological dynamics, as provided by the unifying framework of the 'metacommunity speciation model'.

The current study used the species-rich model taxon Gastropoda to assess how extant communities in Lake Ohrid are structured by performing process-based metacommunity analyses. Specifically, the study aimed at (1) identifying the relative importance of the three community assembly processes and (2) to test whether the importance of these individual processes changes gradually with lake depth or discontinuously with eco-zones shifts.

Based on automated eco-zone detection and process-specific simulation steps, we demonstrated that dispersal limitation had the strongest influence on gastropod community composition. However, it was not the exclusive assembly process but acted together with the other two processes – environmental filtering and species interaction. The relative importance of the community assembly processes varied both with lake depth and eco-zones, though the processes were better predicted by the latter.

This suggests that environmental characteristics have a pronounced effect on shaping gastropod communities via assembly processes. Moreover, the study corroborated the high importance of dispersal limitation for both maintaining species richness in Lake Ohrid (through its impact on community composition) and generating endemic biodiversity (via its influence on diversification processes). However, according to the metacommunity speciation model, the in-

ferred importance of environmental filtering and biotic interaction also suggests a small but significant influence of ecological speciation. These findings contribute to the main goal of the SCOPSCO deep drilling initiative – inferring the drivers of biotic evolution – and might provide an integrative perspective on biological and limnological dynamics in ancient Lake Ohrid.

1 Introduction

Ancient Lake Ohrid on the Balkan Peninsula (Fig. 1) is the oldest and most speciose freshwater lacustrine system in Europe (Albrecht and Wilke, 2008; Neubauer et al., 2015). Recently, an International Continental Scientific Drilling Program (ICDP; Wagner et al., 2014) has been conducted in the lake within the research initiative Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO). One of the major goals of this collaborative project is to infer the drivers of speciation by linking the geological and biotic evolution of the lake over space and time. Geological, limnological, and paleontological data from sediment cores are being complemented with phylogenetic and molecular clock data derived from DNA information of extant endemic species.

Though the sediment and molecular data are still being analyzed, first results indicate that climatic, geological, and/or environmental changes over time may have had little direct effect on speciation and extinction processes in selected endemic biota of Lake Ohrid (Föller et al., 2015). Instead, such changes potentially affected abundances of paleospecies and community compositions over time (Albrecht et al., 2010; Belmecheri et al., 2009; Jovanovska et al., 2016; Reed et al., 2010; Wagner et al., 2014). Horizontal and vertical (bathymetric) environmental gradients may not only have

shaped the structure of extant Ohrid communities (Hauffe et al., 2011; Lorenschat and Schwalb, 2013), but also fostered species divergence (Schreiber et al., 2011; Wysocka et al., 2008). Speciation and extinction, in turn, may have also affected the spatial structure of extant communities (Hauffe et al., 2011).

For Lake Ohrid, these results question the direct effect of climatic, geological, and/or environmental factors on diversification and call for a holistic perspective involving evolutionary processes (e.g., speciation) and ecological processes affecting community composition (e.g., dispersal limitation, species interaction).

Such a mechanistic and unifying eco-evolutionary framework – the metacommunity speciation model – was recently proposed by Hubert et al. (2015). It considers how a metacommunity (i.e., a network of local communities linked by dispersal of multiple interacting species; Leibold et al., 2004) is affected by speciation and vice versa.

In principle, a local community is structured by three non-exclusive consecutive processes (e.g., Leibold et al., 2004; van der Plas et al., 2014): (1) dispersal of individuals to a patch previously unoccupied by the species, (2) environmental filtering that permits the establishment of species whose ecological niche fits the local environmental conditions, and (3) species interaction including competitive exclusion among resident and colonizing species because of shared resources, predators, and/or pathogens.

From a theoretical point of view, all of these three processes might affect speciation (Hubert et al., 2015). However, their individual contribution and spatial dynamics in Lake Ohrid remain little understood. The latter is particularly true for the bathymetric structure of Lake Ohrid. The deep lake has a distinct horizontal eco-zonation (reviewed in Albrecht and Wilke, 2008). This leads to the question whether the individual importance of the three processes mentioned above gradually changes with lake depth or whether there are abrupt changes related to transitions between eco-zones. Conceptually, a differentiation between gradual and abrupt changes in structuring processes among eco-zones may shed light on how limnological complexity and stability affect community assembly and diversification processes.

Gastropods are a suitable model taxon to study community structuring processes as they represent the most species-rich animal group in Lake Ohrid with 74 described species, 56 endemic to the lake and its catchment (Albrecht et al., 2014; Albrecht and Wilke, 2008; Hauffe et al., 2011; Radoman, 1985). In the current study we therefore focus on the question how extant gastropod communities are assembled by performing process-based metacommunity analyses. Our working hypothesis is that, in general, dispersal limitation plays a crucial role in structuring communities.

Our specific aims are:

1. To identify the relative importance of the three community assembly processes (dispersal limitation, envi-

ronmental filtering, and species interaction) in shaping the lakes' gastropod community composition. We simulated community assembly and measured the respective simulation steps corresponding to these three processes.

2. To test whether the importance of these individual processes changes gradually with lake depth or whether they are distinctively related to eco-zones. We first performed an automatic detection of eco-zones based on community composition and then inferred whether the relative importance of the three community assembly processes was better predicted by either lake depth or delineated eco-zones.

This study will help to infer the drivers of community assembly and speciation in Lake Ohrid by providing an independent and unifying view of eco-evolutionary processes and their relationships to ecosystem characteristics. The novel process-based model presented here may also serve as a basis for studies of the community composition and their underlying assembly processes in (paleo)species communities of Lake Ohrid, other ancient lake systems, or elsewhere.

2 Material and methods

2.1 Gastropod sampling and taxonomic classification

The current study is based on gastropod community compositions taken from Hauffe et al. (2011), which were supplemented with additional field data obtained from 2010 to 2011. In total, we analyzed 264 localities of Lake Ohrid and its feeder springs. Gastropods were collected by hand picking, sieving, or dredging from small boats or the research vessel of the Hydrobiological Institute Ohrid. The latter enabled sampling depths of down to 70 m, thus covering the entire bathymetric range of gastropods in Lake Ohrid.

Though phylogenetic relationships among endemic gastropod taxa of Lake Ohrid are increasingly well characterized, a complete picture is still lacking. We classified taxa in five hierarchical levels: species, genus, species flock, family, and superfamily. Note that we used the level 'species flock' for endemic clades that comprise more than one genus (Föller et al., 2015; Wilke et al., 2007). Species flocks typically evolved within the lake and are common in Lake Ohrid. For critical taxa we here used the taxonomic assignments of Bodon et al. (2001), Hubendick and Radoman (1959), and Radoman (1983). We calculated pairwise taxonomic distances between the 66 collected gastropod species using the taxonomic classification above. This method was described by Clarke and Warwick (1998) and is implemented in the package `vegan` v2.2-1 (Oksanen et al., 2015) for the R v3.1.2 statistical environment (R Core Team, 2015).

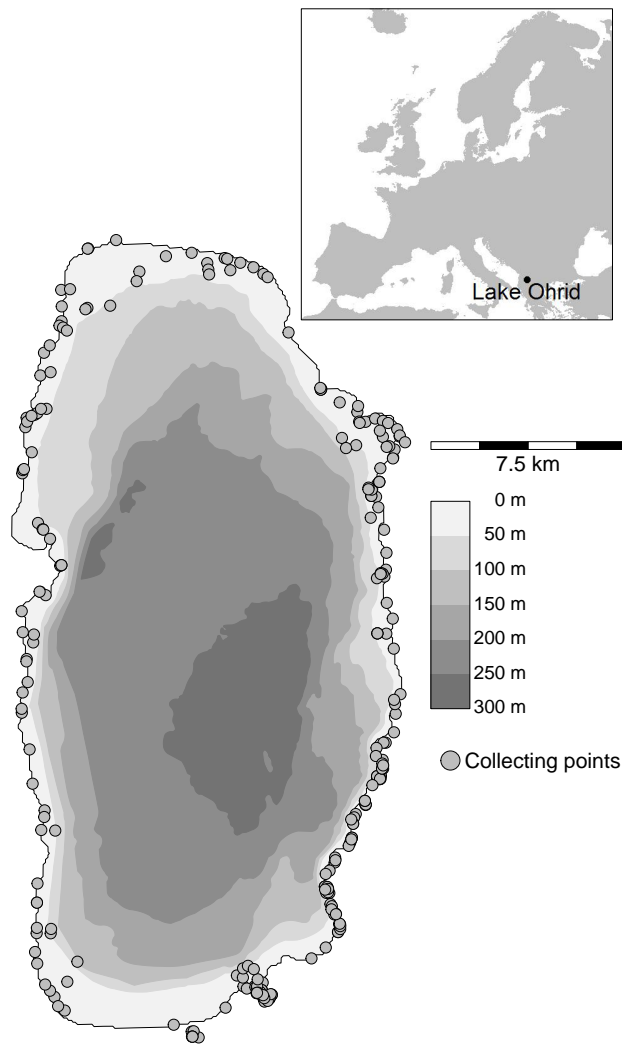


Figure 1. Bathymetric map of Lake Ohrid (Albania, Macedonia) with sampling localities of gastropod communities studied.

2.2 Simulation of individual community assembly processes

Processes of community assembly can be inferred by three distinct approaches. First, environmental parameters and measures of spatial autocorrelation are linked to community composition and may represent proxies for estimating indirectly the importance of processes such as environmental filtering (Sharma et al., 2011) and dispersal limitation (Legendre et al., 2005). Second, a comparison of the phylogenetic structure or trait distribution of a community with a null model of the expected structure or distribution informs about prevailing importance of environmental filtering or species interaction (Webb et al., 2002). Third, a simulation method of stepwise community assembly (STEPCAM) infers the rel-

ative importance of all three processes (van der Plas et al., 2015). It prunes the regional species pool to the size of an observed community by sequentially removing species according to specific simulation processes for dispersal limitation, environmental filtering, and biotic interaction.

The simulation requires a presence-absence matrix of community composition and species characteristics such as traits or their taxonomic/phylogenetic relationship (Fig. 2a). We here extended the original STEPCAM approach, which only considers continuous species traits, and now allow a mixture of continuous and categorical species traits resulting in matrices of pairwise distance between species (Fig. 2a). This generalization also permits the use of phylogenetic or taxonomic distances. These distances are typically strongly correlated with trait divergence among species and used in analyses of community assembly (Emerson and Gillespie, 2008; Webb et al., 2002).

Trait or taxonomic characteristics of a community define the target of the STEPCAM model: if the values of trait/taxonomic indices of a simulated community approximate the observed ones, we assume that the performed species removal steps during the simulation reflect the relative importance of the three assembly processes for the observed community (see specific aim 1). The similarity between simulated and observed communities ($\text{Fit}_{\text{total}}$; van der Plas et al., 2015) is the sum of absolute differences between four indices (i.e., richness, evenness, divergence, and mean distance to the community centroid; Fig 2b) based on traits (Villéger et al., 2008) or phylogenetic/taxonomic distances (Helmus et al., 2007). However, calculating ($\text{Fit}_{\text{total}}$) is problematic because the scale of the utilized indices differs: 'evenness', for example, is bounded between 0 and 1, whereas 'richness' lacks an upper limit. Therefore, van der Plas et al. (2015) standardized the trait indices by dividing them by the standard deviation (SD) of the respective index, calculated for all observed communities. For large differences in species richness or few sampled communities, this approach can be biased because some indices are not independent of species richness (Villéger et al., 2008) and the SD is less precisely estimated in case of small sample sizes. We estimated all SDs using an initial simulation of 500 communities based on observed species richness.

STEPCAM simulates dispersal limitation by randomly removing species with a probability inversely related to their relative frequency in the regional species pool (Fig. 2c). Dispersal limited species are therefore less likely present in the simulated community (van der Plas et al., 2015).

Environmental filtering and species interaction depend on the ecology of the species (i.e., its niche). These ecological requirements are assumed to be reflected by morphological features, which are typically under selection, or effected by the relatedness of species. Environmental filtering therefore predicts that species of a community show similar morphological traits or are closely related because environmental conditions only allow the establishment of species that are

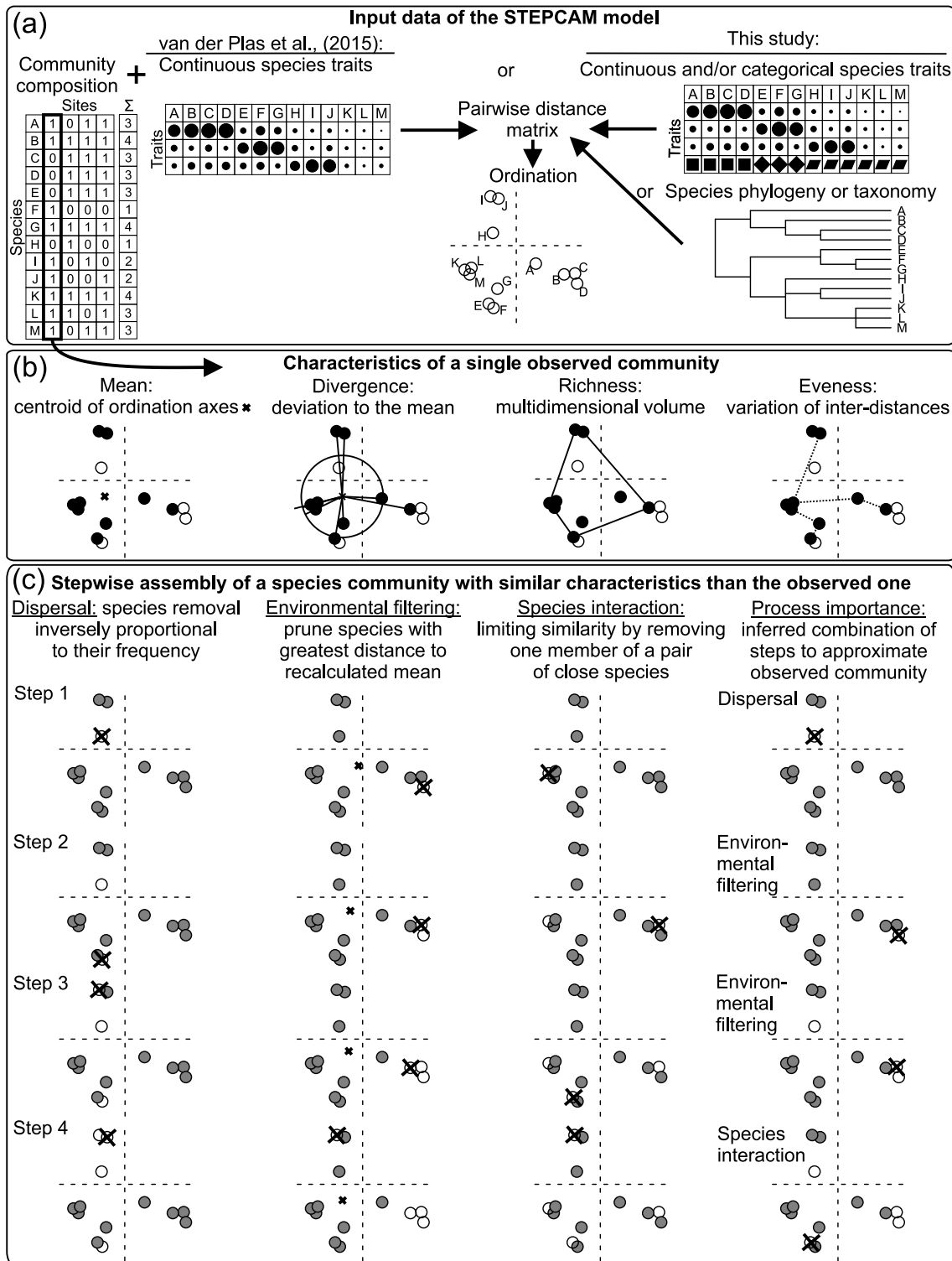


Figure 2. Illustration of the distance-based stepwise community assembly model (STEPCAM). (a) The model is parameterized by species' frequencies and either functional species traits, a species phylogeny, or a hierarchical taxonomic classification. (b) Functional or phylogenetic/taxonomic indices (for details see Villéger et al., 2008) characterize the focal species community. (c) These index-values are the targets for the modeled community. A simulation starts with all species of the regional species pool, removes stepwise species according to the three processes dispersal limitation, environmental filtering, and species interaction, and stops when the same number of species as in the focal community is reached. Approximate Bayesian Computation within a Sequential Monte Carlo framework infers the combination of simulation-steps that generates a species community with minimum differences between observed and generated index-values. The number of removal steps informs about the importance of the respective assembly process.

adapted to the specific habitat (Webb et al., 2002). Pruning species most distant to the morphologically or taxonomically mean of the generated community simulates environmental filtering (Fig. 2c).

Community composition driven by species interaction assumes that species with similar niches do not co-exist because they share the same resources, predators, or pathogens (Webb et al., 2002). Therefore, this process is simulated by removing one of two species from the regional species pool that show the highest similarity in their traits or taxonomy (Fig. 2c).

Following van der Plas et al. (2015), we here utilized Approximate Bayesian Computation within a Sequential Monte Carlo framework (ABC-SMC) for inferring the number of species removals needed per simulation step, which results in a simulated community that approximates the observed community.

Our distance-based community simulations built on the R package STEPCAM v1.0 (Janzen and van der Plas, 2014). We improved the algorithm for runtime and a commented, fully reproducible analysis including the taxonomic distance and presence-absence matrix of gastropod community composition is available in the Supplement. The STEPCAM target for the assembly simulation for each of our 264 sampled communities was a final acceptance rate of 1 in 10 000 simulated communities.

2.3 Testing for gradual vs. distinct changes among eco-zones

For testing whether the importance of individual structuring processes changes gradually with lake depth or discontinuously with eco-zone shifts (see specific aim 2), reliable information for the spatial distribution of these zones is necessary.

Previous assessments of the vertical distribution of eco-zones in Lake Ohrid were based on analyses of habitat types, limnological features, and/or typical species assemblages (Albrecht and Wilke, 2008; Hauffe et al., 2011). In contrast, only a rough approximation of the horizontal dimension exists so far (Stanković, 1960).

Therefore, we first performed an automatic detection of eco-zones using a spatially constrained clustering of ecological networks (Miele et al., 2014). The analysis, implemented in the R package *geoclust* v0.2.0 (Miele et al., 2014), is based on the similarity of gastropod community composition and their geographical connectivity in horizontal (X and Y) and vertical (Z) dimensions. Community composition similarity was calculated using Bray-Curtis distances and the *vegan* package. Similarities were then arc-sin transformed to ensure normality, as required for ecological networks. The three-dimensional spatial network was based on vertical (bathymetric) connectivity and the cost-distance between collecting points along isobaths. The latter approach had to be used because intralacustrine dispersal of benthic organisms is not well approximated by straight line distances (Heino et al.,

2015a). We explored the robustness of our analysis by varying the number of directly connected neighbors from 15 to 264 with an increment of 10, ensuring a fully linked spatial network. For the vertical scale, a connectivity threshold of 8.2 m was determined by a multivariate community correlogram with 9999 permutations in *vegan*, showing that similarity between gastropod communities decreases significantly if their bathymetric distance exceeds this threshold.

In a final step, we used a Bayesian generalized linear model (BGLM; R package *MCMCglmm* v2.21; Hadfield, 2010) to test whether our multivariate response, i.e., the relative importance of the three community assembly processes, was better predicted by either lake depth or delineated eco-zones (see specific aim 2). As decision criterion between the two competing BGLMs, we utilized the deviance information criterion (DIC), a Bayesian measure of model fit (Spiegelhalter et al., 2002). In both BGLMs, we included species richness and its interaction with lake depth or eco-zones as additional predictor because process-importance may co-vary with species richness. Prior to model fitting, normality of the $[0, 1]$ scaled multivariate response was improved by an additive planar transformation, implemented in the compositions v1.4-1 package (van den Boogaart et al., 2014) for R.

3 Results

3.1 Relative importance of the three community assembly processes

Using our ABC-SMC-based STEPCAM approach, we obtained a posterior distribution for the relative contribution of the three community assembly processes (dispersal limitation, environmental filtering, and biotic interaction) in shaping the lakes' gastropod community composition. Averaging the posterior distribution over all 264 gastropod communities, dispersal limitation achieved the highest relative importance with 80.1 % (95 % bootstrapped confidence interval (CI): 77.0–83.0), followed by environmental filtering (mean 11.5 %; CI: 9.4–13.8), and species interaction (mean 8.4 %; CI: 7.2–9.7).

3.2 Testing for gradual vs. distinct changes among eco-zones

Prior to testing whether the importance of the three individual processes changes gradually with lake depth or discontinuously with eco-zones shifts, we performed an automatic detection of eco-zones using a spatially constrained clustering of ecological networks. Applying a range of one to ten groups and different numbers of directly connected neighbors in the spatial network, our delineation of eco-zones consistently revealed that seven groups of gastropod communities showed the highest likelihood. These communities relate to seven eco-zones (southeastern (SE) upper littoral 1–3,

non-SE upper littoral, lower littoral, upper sublittoral, lower sublittoral). The horizontal and vertical distribution of these eco-zones based on 65 neighbors is shown in Fig. 3 (zone terminology roughly follows Stanković, 1960).

Finally, we used two BGLMs to test whether the relative importance of the three community assembly processes was better predicted by either lake depth or delineated eco-zones. In general, assembly processes were explained both by depth and eco-zones. However, according to the rule of thumb of Bayesian model selection (Bolker, 2008), the difference in DIC greater than 10 decisively favored eco-zones over lake depth (DIC values of -861 vs. -753 , respectively). For a visual presentation of the eco-zone dependent relative importance of dispersal limitation, environmental filtering, and biotic interaction see Fig. 4.

4 Discussion

In the current study, we addressed the question of how extant gastropod communities are assembled by performing a process-based metacommunity analysis. More specifically, we attempted to identify the relative importance of three previously suggested community assembly processes (dispersal limitation, environmental filtering, and species interaction) and tested whether their importance changes gradually with lake depth or discontinuously with eco-zone shifts. Given that geographical isolation has been stressed as important driver for speciation in Lake Ohrid (reviewed in Albrecht and Wilke, 2008) and adhering to the metacommunity speciation model, our working hypothesis was that dispersal limitation plays also a crucial role in structuring communities. We, indeed, could show that dispersal limitation had the strongest influence on gastropod community composition in Lake Ohrid. However, it was not the exclusive assembly process but acted together with the other two processes – environmental filtering and species interaction (Fig. 4). In fact, the relative importance of the three community assembly processes varied both with lake depth and eco-zones (Fig. 4), though the processes were better predicted by delineated eco-zones.

In the following, these principal findings are interpreted in the context of how ecosystem features influence community assembly. We also discuss the implications of our three community assembly processes for patterns and processes of speciation in endemic gastropods of Lake Ohrid. As structuring processes appear to be strongly related to eco-zones, we first address the result of our automatic eco-zones identification.

4.1 The eco-zones of Lake Ohrid

Previously, six horizontal and four vertical eco-zones have been suggested for Lake Ohrid (Stanković, 1960; Albrecht and Wilke, 2008). However, as they were largely based on an a priori differentiation into horizontal and vertical features,

we here automatically delineated eco-zones using a three dimensional approach (i.e., involving the three spatial axes X , Y , and Z).

The zonation inferred (Fig. 3) resembles, in large parts, the one previously proposed. However, it appears to be slightly more complex in terms of horizontal and vertical structuring. Moreover, the zones show a considerable degree of overlapping, reflecting the patchy nature of some habitats in the lake (see Albrecht and Wilke, 2008). The strong vertical structure largely corresponds to vertically arranged biotopes in Lake Ohrid, such as the ‘*Chara* belt’ in the lower littoral and the ‘shell zone’ in the upper sublittoral (Albrecht and Wilke, 2008). Note that in this study we could not identify a potential fifth vertical zone, the profundal, as the only species of gastropod previously reported from there has not been found in years (Hauffe et al., 2011).

Interestingly, we do not see any significant horizontal structuring within deeper vertical zones. However, within the upper littoral (i.e., a zone typically extending from 0 to 3 m water depth), a strong horizontal structure is evident. One eco-zone (‘non-SE upper littoral zone’) comprises all shallow water gastropod communities from the northeastern, northern, western, and southwestern parts of the lake. Three additional eco-zones can be found in the southeastern upper littoral (‘SE upper littoral zones 1–3’). This area, comprising major spring fields within the lake, has long been known for its high degree of point-endemism (Albrecht et al., 2006; Albrecht and Wilke, 2008; also see Hauffe et al., 2011 Fig. 3a for compositional similarities among these communities).

The emergent pattern of partly overlapping horizontal/vertical eco-zones, indeed, confirms that the gastropods of Lake Ohrid adhere to the metacommunity concept.

4.2 Relative importance of community assembly processes

Our results suggest that gastropod communities of Lake Ohrid are substantially structured by the dispersal limitation process (i.e., restricted specimen exchange; mean importance across all communities $\sim 80\%$; see Fig. 4). Environmental filtering and biotic interaction were of lower importance (12 and 8%, respectively). However, the individual importance of these three processes depends on lake depth and even more on individual eco-zones (Fig. 4). The importance of dispersal limitation is, for example, relatively low in the SE upper littoral 1 (i.e., the shallowest and most species rich zone in Lake Ohrid) and in the lower sublittoral (i.e., a deep and relatively species poor zone in Lake Ohrid). The opposite is true for environmental filtering and, to a lesser extent, for species interaction (see Fig. 4). This interesting relationship shows that the relative importance of the three community structuring processes does not depend on species richness or lake depth *per se*. The latter might also explain why eco-zones (i.e., three spatial dimensions) have a higher explanatory power than lake depth (only one spatial dimensions).

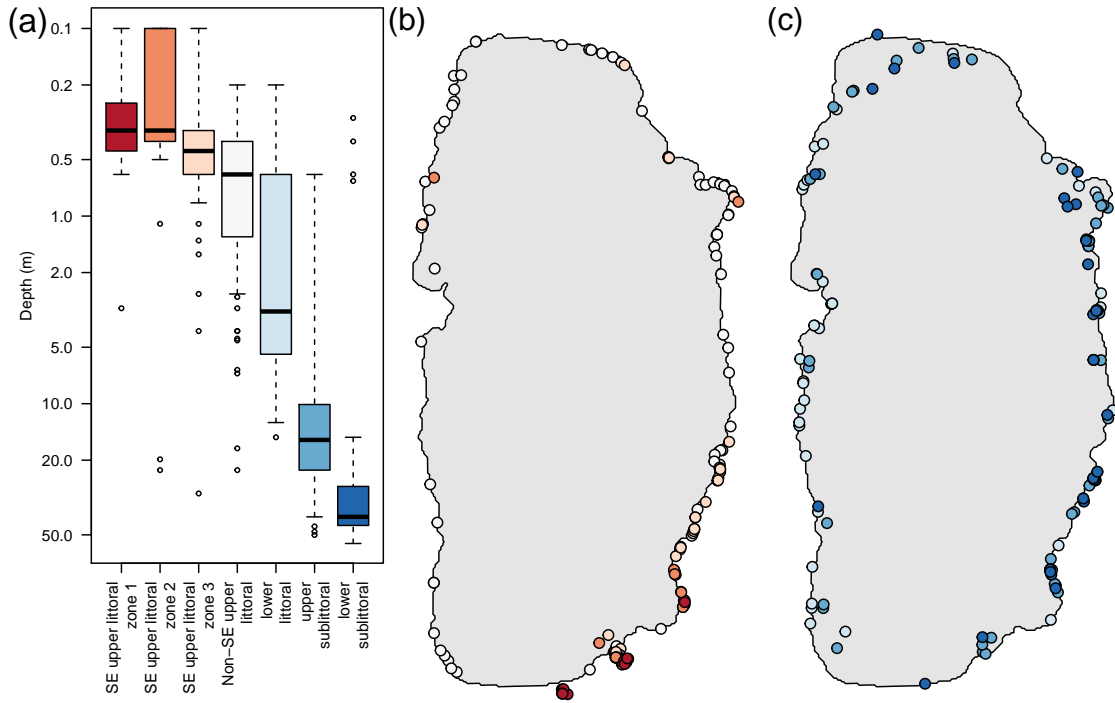


Figure 3. Sampling sites and eco-zonation of 264 gastropod communities of ancient Lake Ohrid and its feeder springs. Eco-zones were detected by network analysis weighting links among sampling sites by their geographical proximity and compositional similarity. (a) Vertical (bathymetrical) extension of the eco-zones. Due to the spatial density, plots of horizontal distribution of clusters were divided into (b) upper littoral, and (c) lower littoral and sublittoral.

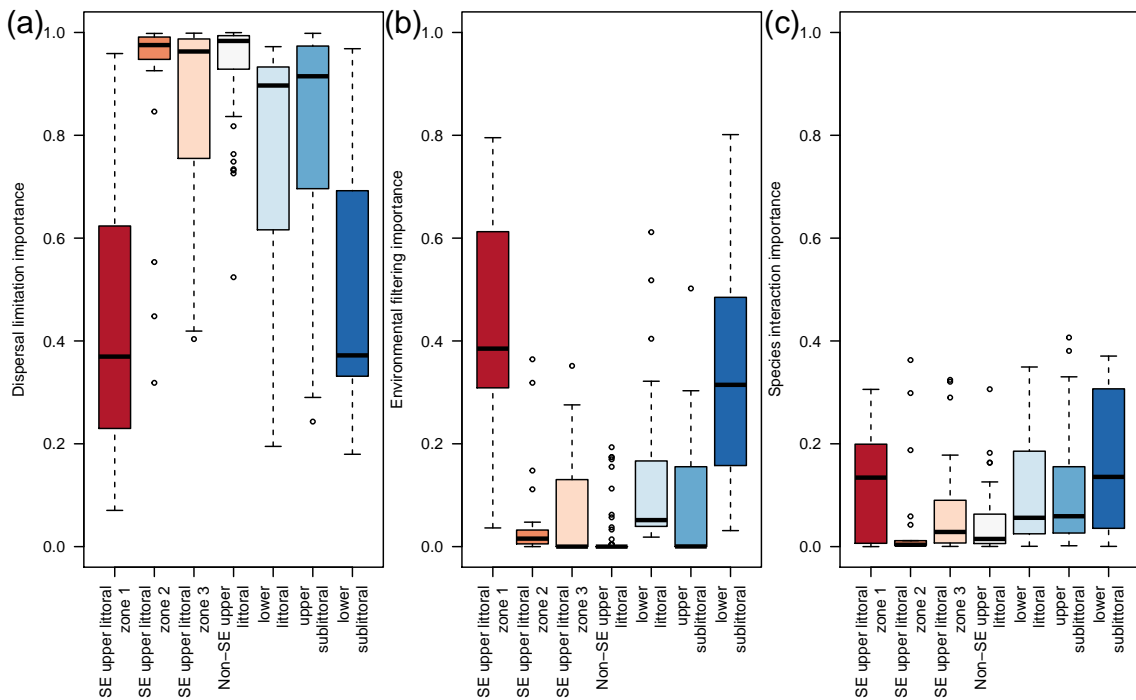


Figure 4. Box plots showing the eco-zone dependent relative importance of (a) dispersal limitation, (b) environmental filtering, and (c) biotic interaction in structuring gastropod communities. Colors correspond to Fig. 1. These differences in process-importance due to eco-zones are statistically supported by a multivariate Bayesian generalized linear model.

Interestingly, the clearly demonstrated high importance of dispersal limitation for maintaining species richness in Lake Ohrid through its impact on community structure stands in contrast to some other studies on Lake Ohrid biota. In fact, previous investigations on gastropod (Schneider et al., 2014), ostracod (Lorenschat et al., 2014), diatom (Reed et al., 2010), and fungal communities (Čomić et al., 2010) suggested a strong environmental control (= environmental filtering) of community composition. However, this is not surprising as other processes were not considered in these studies.

In studies that did consider more than one process, the picture was more complex and showed in addition to environmental filtering, also the influence of dispersal limitation and/or species interaction. This concerns gastropod communities in Lake Ohrid (Hauffe et al., 2011) and in other ancient lakes such as Lake Tanganyika (Meyer et al., 2011), but also communities in freshwater systems in general (Heino et al., 2015b).

In a comparable study, Janzen et al. (2016) investigated cichlid communities in Lake Tanganyika. Interestingly, the individual importance of the assembly processes inferred is very similar to ours, with dispersal limitation being the dominant process. In contrast to our study, they did not find a correlation of process-importance with environmental characteristics. The reasons for this difference remain unclear, though differences in the life-history of the study taxa and in the spatial extent of the study area (Janzen et al., 2016 performed a local study) may play a role.

As the importance of assembly processes often depends on spatial scale (Meyer et al., 2011) and resolution (Münkemüller et al., 2014), the sensitivity of the STEPCAM approach to spatial data aggregation should generally be considered. However, as the spatial resolution in our study is relatively high and as dispersal and movement rates of freshwater gastropods are generally low (Kappes and Haase, 2012; Michel et al., 2007), we here refrained from data aggregation. Note that the occurrence of invasive species, which often have high dispersal rates, could have affected the STEPCAM analysis. However, only two recent gastropod invasions of limited spatial extensions are known from Lake Ohrid (Albrecht et al., 2014) and should therefore not have biased our analysis.

4.3 Metacommunity implications for gastropod speciation

If we accept that species divergence and community assembly can be unified in an eco-evolutionary framework because both are based on similar processes (Hubert et al., 2015), then the here inferred importance of processes allows for a fresh look on the diversification mode of Lake Ohrid's endemic gastropods. Research on species divergence, in general, and in ancient lakes in particular, has traditionally focused on geographic speciation (Cristescu et al., 2010; Schluter, 2001;

also see Albrecht and Wilke, 2008 for a review on geographic speciation modes in Lake Ohrid). Adaptive diversification along environmental gradients, however, highlights the additional role of ecology in driving species divergence in ancient lakes (Schön and Martens, 2004).

Our results support this perspective of non-exclusive geographic and ecological speciation in Lake Ohrid. Though the inferred high importance of dispersal limitations in structuring gastropod communities implies a dominant role of geographic speciation in the lake (also see Albrecht et al., 2006; Kilińska et al., 2013; Trajanovski et al., 2010; Wysocka et al., 2014), the demonstrated importance of environmental filtering and species interaction suggests a small but significant influence of ecological speciation.

The fact that ecological speciation appears to be more important both in the SE upper littoral 1 (i.e., a shallow and species-rich zone) and in the lower sublittoral (i.e., a deep and species-poor zone) potentially implies a bimodal contribution of ecological speciation in generating biodiversity over time.

4.4 Methodological implications and outlook

For many questions concerning processes in eco-evolutionary biology, such as dispersal- or selection-dependent species diversification (Pigot et al., 2010) and community assembly (Rosindell et al., 2015), no analytical solutions are (yet) available. However, the outcome of processes can be simulated by utilizing a wide range of parameter values representing them. The set of parameters resulting in a simulated pattern that resembles the observed one best is then assumed to approximate the processes in question. Our newly developed distance-based STEPCAM approach is a relatively simple model that could be easily extended by making, for instance, dispersal limitation spatially or temporally explicit, but at the risk of overparameterization.

Moreover, we suggest further exploration of the STEPCAM approach using different taxa in Lake Ohrid, for instance in another species rich-group, the diatoms. A combined study of extant and paleo-communities derived from multiple sediment cores would allow inferring the relative importance of dispersal limitations, environmental filtering, and species interaction over space and time.

5 Conclusions

Our study builds on a prediction of the metacommunity speciation model: if geographic speciation is the prevailing mode of species divergence, as suggested by many evolutionary studies, then dispersal limitation should also structure communities. The results of our analysis corroborate this hypothesis for gastropods in Lake Ohrid. The inferred importance of environmental filtering and biotic interaction in

community assembly also suggests a small but significant influence of ecological speciation on diversification dynamics; an aspect which previously could not be quantified. Moreover, based on a novel automated detection of eco-zones in Lake Ohrid we show that these eco-zones do influence the relative importance of community assembly processes, whereas former studies could only show that these limnological features give rise to distinct community composition. These findings contribute to the main goal of the SCOPSCO initiative – inferring the drivers of biotic evolution – and provide an integrative perspective on biological and geological dynamics in ancient Lake Ohrid.

Moreover, our novel distance-based STEPCAM complements the growing eco-evolutionary toolbox that aims at disentangling patterns and processes.

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Author contributions. T. Hauffe conceived the study. C. Albrecht and T. Hauffe collected and identified specimens. T. Hauffe performed the analyses. TH and TW wrote the manuscript with contributions from all co-authors. All authors gave final approval for publication.

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