Scale dependent niche conservatism found in a lake fish community

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Abstract

Investigations to niche evolution have received controversial results in recent times, leading to some confusions in ecological studies: competitive exclusion principle (CEP) predicts that closely related species should be adequately divergent; while niche conservatism (NC) predicts that closely related species should be ecologically most similar. In the present study, by using stable isotope to signify trophic niche, we analyzed niche divergences of 57 fishes from a lake (Poyang Lake, central China) at the phylogenetic scale, as well as niche divergences and overlaps of 7 fishes (same subfamliy) at 5 sites of this lake, and comprehensively investigated the concepts of NC and competitive exclusion principle (CEP). The results showed that, NC exists on a large scale (trophic differences showing positive relationships with genetic distances), but not at the local scale (sister species showing larger differences than closely related species, and almost no trophic overlap), where the CEP works better. Besides, trophic convergence was also found between some very distantly related species, leading to the possible limited divergence. We believe these findings will contribute to future theoretical and empirical niche explorations.

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Abstract: Investigations to niche evolution have received controversial results in recent times, leading to some confusions in ecological studies: competitive exclusion principle (CEP) predicts that closely related species should be adequately divergent; while niche conservatism (NC) predicts that closely related species should be ecologically most similar. In the present study, by using stable isotope to signify trophic niche, we analyzed niche divergences of 57 fishes from a lake (Poyang Lake, central China) at the phylogenetic scale, as well as niche divergences and overlaps of 7 fishes (same subfamliy) at 5 sites of this lake, and comprehensively investigated the concepts of NC and competitive exclusion principle (CEP). The results showed that, NC exists on a large scale (trophic differences showing positive relationships with genetic distances), but not at the local scale (sister species showing larger differences than closely related species, and almost no trophic overlap), where the CEP works better. Besides, trophic convergence was also found between some very

distantly related species, leading to the possible limited divergence. We believe these findings will contribute to future theoretical and empirical niche explorations.

Keywords

Stable isotope, Trophic niche, Competitive exclusion principle, Phylogenetic scale

Introduction

The concept of ecological niche is fundamental in ecology, explorations to which have greatly prompted the advances of ecological science. Traditionally, studies on this concept have been focused on the ecological aspect, with the core parts being the understanding of species coexistence mechanism, or the famous competitive exclusion principle (CEP). It states that "two species with identical niches (and compete for a single resource) cannot coexist together indefinitely" (Gause, 1934; Hardin, 1960; De León et al. , 2014). According to this, closely related species should be adequately divergent (Svensson, 2012; Wang et al. , 2015; Liu et al. , 2018; Silva et al., 2020). The CEP has so much influential on the whole ecological studies that almost all theoretical investigations and empirical data explanations are based on it (MacArthur, 1958; Holt, 2013).

However, in some recent times, niche evolution or niche divergence has drawn great attention resulting in a new principle of niche conservatism (NC) (Webb et al., 2002; Ackerly, 2003; Ackerly et al., 2006; Kraft et al. , 2007; Swenson & Enquist, 2009). According to it, a species tends to retain aspects of its fundamental niche over space and time, therefore, closely related species should be ecologically most similar (Harvey & Pagel, 1991; Losos et al., 2003; Wiens & Graham, 2005; Diniz-Filho & Bini, 2007). Apparently, these two principles (CEP and NC) have some contradictions on their predictions to niche relationships of closely related species.

At present, due to the longer research history, the CEP has been investigated extensively and accepted as a general rule (Davydova et al., 2003; López-Gómez & Molina-Meyer, 2006; Hening & Nguyen, 2020). However, studies on the NC over macroevolutionary time have received different results. Supports for NC have been found in amphibians (Hu et al., 2016), freshwater arthropods (Morinièreet et al., 2016) and plants (Ricklefs & Latham, 1992; Prinzing et al., 2001; Crisp et al., 2009; Liu et al., 2012, 2015), while contradictions found in studies such as microhabitat preferences in *Anolis* lizards (Losos et al., 2003), Eltonian niche of 32 freshwater fishes (Comte et al., 2017), climatic, habitat and trophic niches of a European avian assemblage (Pearman et al., 2014). Therefore, given all the contradictions, it has not been explored whether CEP and NC can be synthesized together.

In the present study, by using stable isotope analysis to signify trophic niche and represent species ecological niche of 57 fish species in 13 families and 10 orders collected from the Poyang Lake, central China, we examined niche evolution or conservatism at a phylogenetic scale and test NC at phylogenetic scale. Besides, we analyzed niche divergence among 7 species from a subfamily (Cultrinae, Cyprinidae) to test the CEP by comparing the niche differences and overlaps in their coexisting local sites. We found that the two principles work at different scale: CEP present at local species coexistence scale, while NC present at relatively larger evolutionary scale. Therefore, both two principles can be synthesized in this framework. And this further understanding to niche evolution will be beneficial for theoretical study to species coexistence mechanism and give hints for future conservation.

Material and methods

Study areas and sampling sites

Poyang Lake (28°4'-29deg46'N, 115deg49'-116deg46'E), the largest freshwater lake in China, situated in the south bank of the middle reaches of the Yangtze River (Wu et al., 2021). The lake receives inflows from five tributary rivers in the basin, drains into the Yangtze River at Hukou after regulation and storage (Song et al., 2021). In this study, we collected samples from 5 sites (Hukou County, Xingzi County, Duchang County, Wucheng Town, Poyang County) in the Poyang Lake (Fig. 1).

Sample collection and processing

All fish samples were collected by nets and cages with the help of local fisherman during October to December 2019. Each fish sample was identified to the species level according to Chen (1998), Yue (2000), Chu (1999), and Fishbase (Froese & Pauly, 2018).

A total of 2157 individuals were collected, representing 57 fish species belonging to 13 families and 10 orders (Supplement Appendix 1). After preserving an appropriate amount of muscle tissue in 95% alcohol for molecular analysis, the whole body was fixed in 10% formalin and deposited in the Institute of Hydrobiology, Chinese Academy of Sciences.

For stable isotope analysis, white dorsal muscle was collected and rinsed with distilled water. The cleaned muscle was dried to a constant weight in an oven at 60 for at least 48 h and homogenized to powder by an automatic grinder, which was finally stored in clean centrifuged tubes until analysis.

DNA extraction, PCR amplification and sequencing

Total genomic DNA was extracted using the salt-extraction protocol (Aljanabi & Martinez, 1997). The cytochrome b gene (Cyt *b*) was amplified with the primers L14724 and H15915 (Tang et al., 2012). Each 30 μL reaction volume contained 3 μL 10x Easytaq Buffer, 1.5 μL dNTPs (each 2.5 mM), 0.25 μL Taq DNA polymerase, 1μL each primer, 2 μL template DNA, and 21.25 μL sterile double distilled water. Thermocycling program for the polymerase chain reaction (PCR) included: an initial denaturation at 94°C for 5 min, 35 denaturation cycles at 94°C for 30 s, annealing at 54°C for 45 s, extension at 72°C for 1 min, and a final extension at 72°C for 10 min. PCR products were sent to commercial sequencing companies for purification and sequencing.

Genetic distance and phylogenetic analyse

Multiple alignments of DNA sequences were conducted using Clustal X (Thompson et al., 1997), and manually checked with SEAVIEW (Galtier et al., 1996). Haplotypes collapsed in ALTER (Glezpeña et al., 2010) were used for estimation of phylogenetic trees. The Kimura's 2-parameter (K2P) genetic distances were cuculated using MEGA X (Kumar et al., 2018) for the 57 species.

Based on the sequences of Cyt *b* gene, phylogenetic relationships of 7 Cultrinae species (*Culter erythropterus* , *Culter mongolicus* , *Culter dabryi* , *Culter alburnus* ,*Hemiculter leucisculus* , *Hemiculter bleekeri* ,*Pseudolaubuca sinensis*) were reconstructed using Bayesian inference (BI) and maximum likelihood (ML) approaches. We selected 4 species of Xenocypridinae as the outgroup taxa (*Xenocypris argentea* MH797098, *Xenocypris davidi* MH797100,*Distoechodon hupeinensis* MH797101, *Pseudobrama simoni*MH797105). The best-fit model (GTR+F+G4) of nucleotide substitution for the data was identified by ModelFinder (Kalyaanamoorthy et al., 2017) using the Corrected Akaike Information Criterion implemented in PhyloSuite platform (Zhang et al., 2020). BI and ML analysis were performed with MrBayes v3.2.7 (Ronquist et al., 2012) and IQ-TREE 1.5 (Nguyen et al., 2015), respectively, implemented in the PhyloSuite platform (Zhang et al., 2020). In BI, four simultaneous Markov Chain Monte Carlo (MCMC) were run for 6 million generations sampling every 100 generations, and using a burn-in rate of 25%. In ML analysis, we evaluated the node support by 1000 ultrafast bootstrap replicates (UFBS).

Stable isotope laboratory analysis

Subsamples of muscle tissue (c. 200-300 μg dry mass) were transferred into tin capsules and analysed for carbon and nitrogen stable isotopes using Delta V Advantage mass spectrometer coupled to Flash 2000 HT elemental analyser (Thermo Fisher Scientific, Waltham, MA, USA). Stable isotope ratios were expressed in delta (δ) notation in parts per thousand or per mil ($[(R_{\text{sample}} / R_{\text{standard}}) -1] \times 1000$, where X is ^{13}C or ^{15}N, R_{sample} and R_{standard} are the^{13}C/^{12}C or^{15}N/^{14}N ratios of the sample and standard, respectively. The standard reference materials Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen (Fry, 1999; Mendoza-Carranza et al., 2010; Ricciardelli et al., 2017). USGS40, USGS41, USGS65, USGS41A, UREA-Thermo and IAEA-600 were used as internal reference standards and interspersed in the samples. The analytical precision (quantified via repeated analysis of internal reference standards) was ± 0.2bothδ ^{13}C and δ ^{15}N.

Stable isotope statistical analysis

δ^{13}C-δ^{15}N scatter diagram was used to reflect the trophic niche relationship among 57 species in GraphPad Prism version 5.0. For each species, the ellipse centroid is the mean δ^{13}C andδ^{15}N values among the samples. We then calculated Euclidean distances between ellipse centroids between species, which represents a measure of interspecific isotopic niche differences (Turner et al., 2010) in EXCEL 2019. Two centroids occupied different locations (i.e. different trophic niches) if the Euclidean distance between them is significantly greater than zero (Galetti et al., 2016). A box plot with Mann-Kendall Trend Test can be used to test whether Euclidean distances between ellipse centroids among species exhibit a significant tendency for genetic distance. This statistical analyse was conducted in the R package 'trend'.

To identify the possible niche conservatism (NC) or competitive exclusion principle (CEP), all the data were pooled together, and trophic differences were compared between distantly related species, closely related species and sister species using Two-Related-Samples Nonparametric Test. This analyse was performed using STATISTICA 18.0. In this study, sister species were perceived as the closest relative of each other in the phylogenetic relationships of Cultrinae (e.g. *C. erythropterus* VS *C. mongolicus*). Species in the same clade of Cultrinae were considered as closely related species (e.g. *C. erythropterus* VS *C. alburnus*), and in the different clade of Cultrinae were regarded as distantly related species (e.g. *C. erythropterus* VS *H. leucisculus*). Furthermore, the δ^{13}C and δ^{15}N bi-plots corresponding to trophic niche space were used to reflect the trophic niche relationship of 7 species. Considering the variation in sample size, the corrected standard ellipse areas (SEAc), which accounts for core trophic niche, were calculated based on the corrected isotope data and enclose 40% of the data (Jackson et al., 2011, 2012; Syväranta et al., 2013). The SEAc were used to evaluate the trophic niche width of each species and its distribution in trophic niche space (Yao et al., 2016). In addition, we calculated the overlapping SEAc of the 7 species in each sampled site. The analyses ofδ^{13}C and δ^{15}N bi-plots, SEAc and percentage of SEAc overlap were performed using the R package 'SIBER' and 'SIAR' (Jackson et al., 2011).

Results

Analysis of niche conservatism among the 57 species

In the present study, each of the 57 species showed differences in their niches indicated by the δ^{13}C andδ^{15}N values. In overall, the stable isotope values ranged from -36.707 to -18.129 for δ^{13}C, represented by *Cirrhinus mrigala* and *Misgurnus anguillicaudatus* ; and from 5.184 to 21.525 forδ^{15}N, represented by *Paramisgurnus dabryanus* and *Neosalanx brevirostris* (Fig. 2). Pairwise species niche differences (EDBEC, Euclidean distances between ellipse centroid) ranged from 0.063 to 15.256, with the shortest distance occurring between two bitterling species (*Acheilognathus rhombeus* and *Rhodeus sinensis*), and the most distant between a minnow and a loach, *Pseudolaubuca engraulis* and *Misgurnus anguillicaudatus* (Fig. 3).

The plot of pairwise species trophic niche differences against genetic distances showed a rough positive pattern, indicating possible niche conservatism. Further analysis showed that, the positive relationships were significant while genetic distances less than 0.24, but niche differences may reach saturation and showed a stable trend while genetic distances larger than 0.24. Besides, at the very far genetic distance (Fig. 3, Fig. 4), some species pairs showed very little niche differences, indicating niche convergence. For instance, trophic differences (EDBEC) between *Silurus asotus* and*Siniperca scherzeri* was only 0.35.

In addition, we also found that species niche differences were distributed in skew, with most species pairs (87.22%) bearing not very much differences (EDBEC less than 6), while only a few species pairs (12.78%) had considerable differences in their trophic niches (EDBEC more than 6) (Fig. 5).

Trophic niche evolution of Cultrinae species

Phylogenetic relationships of Cultrinae species

A total of 668 sequences of the complete cytochrome b gene (1,140 bp) were obtained, and 171 haplotypes were identified. Based on these haplotypes, BI tree and ML tree yielded congruent topologies and consistently supported *C. erythropterus* was sister species to *C. mongolicus* , *C. dabryi* sister to *C. alburnus* , and *H. leucisculus* sister to *H. bleekeri* ; then *H. leucisculus* +*H. bleekeri* sister to *Pseudolaubuca sinensis* (Fig. 6).

Trophic niche divergence of Cultrinae species at phylogenetic scale

In overall, when all the data pooled together, the 7 Cultrinae species showed similar niche space, with a lot overlap as well as some differences (Fig. 7). At the phylogenetic scale, to identify the possible niche conservatism, trophic differences were compared between distantly related species, closely related species and sister species. It was found that trophic differences between distantly related species were significantly larger than closely related species (P =0.02 $<$ 0.05), indicating the possible NC (Fig. 8). However, while making comparison between sister species and closely related species, it was found that trophic differences between sister species were larger than those between closely related species (excluding sister species) (not statistically significant, P>0.05), indicating non-NC existing here.

Trophic niche divergence at the local scale

To identify trophic niche competition, niche overlaps were analyzed between all species pairs of the 7 species in the 5 sampling sites respectively. The 7 species may not be present at all the 5 sites. It was found that, some species pairs showed some extent overlaps in their trophic niches, some not. Interestingly, all sister species pairs except one showed no overlap, and the overlaps between sister species were significantly less than those between closely related species (excluding sister species) (P =0.008 $<$ 0.05), indicating the possible competitive exclusion there (Table. 1, Supplement Fig. A1).

Discussion

Niche conservatism

The present study showed that, for the 57 species, in a broad scale, they exhibited niche conservatism. This is consistent with some previous studies. Eaton et al. (2006) plotted ecological differences with genetic distances for 3 clades of American blackbirds, resulting very similar patterns as in our present study, and concluded with a general pattern of niche conservatism. However, they did not do statistic test for these relationships. In our present study, we conducted statistic tests and found that, when genetic distances were small, there were significantly positive relationships between niche differences and genetic distances; while genetic distances were large, niche differences may reach saturation and showed a stable trend.

Based on these results, on the one hand, we proposed that there is a general pattern for niche conservatism, leading to the positive relationships between niche differences and genetic distances, especially when the genetic distance is within some limits. On the other hand, we proposed that, there is a limit restricting the divergence. In our present study, when genetic distances were above 0.24, the pairwise species differences reached saturation and showed a rather stable trend. Besides, distribution pattern of niche difference also showed that most species pairs were with limited divergence, only a few species were with large difference. We think that this is because that there are only limited trophic resources in the environment, leading to the limited niche divergence and trophic niche convergence.

Niche divergence and competition

The present study showed that, at the local scale, sister species showed larger divergence than closely related species, almost all sister species pairs showed no overlap, and the overlaps between sister species were significantly less than those between closely related species, which is consistent with the competition exclusion principle. Niche divergence has been found to be important in maintaining diversity, initiating and completing speciation. The present results provide data well supporting the existing viewpoints.

Scale dependent niche evolution

Ecological niche is an important concept for investigating core ecological problems such as species coexistence, community assembly rules. Understanding how niche divergence (evolving) will be beneficial for theoretical study to species coexistence mechanism and make predications for species distribution and community structure, give hints for future conservation. Previous studies have provided evidences supporting niche conservatism. For example, based on field experiments with 32 plant species, Burns & Strauss (2011) proposed that more closely related species are more ecologically similar. Culumber & Tobler (2016) found that closely related species in the two swordtail clades exhibited higher levels of niche overlap than expected given environmental background similarity indicative of niche conservatism. Hadly et al. (2009) suggested niche conservatism above species level (genera and families) of North American mammals.

However, counter evidences were also provided by some authors. After comparing geographical parameters with molecular phylogenetic distances, Knouft et al. (2006) found that no general relationship exists between phylogenetic similarity and niche similarity, with some examples in which closely related species display niche conservatism and some in which they exhibit highly divergent niches. Losos et al. (2003) also suggested niche lability in the evolution of a Caribbean lizard community. Pearman et al. (2014) proposed no evidence for past phylogenetic niche conservatism of a European avian assemblage in climatic, habitat and trophic niches.

For these controversial results, Crisp & Cook (2012) stressed that phylogenetic niche conservatism is a pattern, not a process, and is found only in some traits and some lineages. Wang et al. (2015) also mentioned that different dimensions of ecological niche may display different evolutionary patterns.

According to our present results, we propose that niche evolution could be dependent not only on niche dimensions, but also on scales. On a large scale, niche may exhibit conservatism; while on a small scale, especially when the species co-exist in one local area, competitive exclusion principle may work, and the very closely related species may exhibit larger niche divergence. It is interesting to note that some very distantly related species showed trophic niche convergence in the present study. We guess that these distantly related species could have evolved differences in different niche dimensions, so they could share similar trophic niche. In overall, we believe that our findings will contribute to future theoretical and empirical niche explorations.

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