Geographical and temporal origins of Neocaridina species (Decapoda: Caridea: Atyidae) in Taiwan

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Research article

Keywords: DNA barcoding, Neocaridina, origin, phylogeography, approximate Bayesian computation

Posted Date: July 29th, 2019

DOI: https://doi.org/10.21203/rs.2.12048/v1

Version of Record: A version of this preprint was published on November 21st, 2019. See the published version at https://doi.org/10.1186/s12863-019-0788-y.

Abstract

Background The freshwater species in Taiwan Island have been documented originated from mainland China and Japan Islands multiple times and by multiple colonization routes. Moreover, the sequences from mitochondrial DNA cytochrome c oxidase subunit I (COI) have been used as DNA barcoding to identity species. This study used the COI sequences to identify Neocaridina species in Taiwan and examine their geographical and temporal origins. Results In total, 479 specimens were collected form 35 localities, which almost covers all rivers in Taiwan. The ML tree displayed that all sequences were assorted into 13 taxa (clades), and all sequences in Taiwan were assorted into four clades. The Bayesian skyline plots revealed that these four Neocaridina species in Taiwan declined recently. Conclusions All results support that (1) there are four Neocaridina species in Taiwan and they correspond to N. davidi, N. saccam, N. ketagalan and an undescribed Neocaridina species (N. sp.); (2) these four species colonized Taiwan Island by four colonization events; (3) N. sp. colonized Taiwan before the Taiwan Island developed its shape and then restricted in East Taiwan; (4) after the island reached its shape, N. ketagalan and N. saccam colonized Taiwan from Japan Islands and mainland China, respectively; (5) N. davidi colonized northern Taiwan lastly; and (6) the cyclic glacial and landform changes shaped the colonization events and population structures of Neocaridina species.

Background

The genus *Neocaridina* Kubo, 1938, is a group of land-locked species of the family Atyidae, consisting of 26 species and distributed in East Asia [1, 2]. Based on the Taiwanese atyid shrimp fauna [3, 4] only one species, *N. denticulate*, is distributed throughout Taiwan Island. Shih and Cai [5] proposed two new species, *N. saccam* and *N. ketegalan*, in South and North Taiwan, respectively. However, Shin and Cai [5] only sampled the specimens of *N. ketegalan* in one population and that of *N. saccam* in two populations. Thus, our study wanted to know how many *Neocaridina* species are there and the distribution pattern of each species in Taiwan.

Taiwan Island is located off the southeast coast of mainland China and is separated from China by the shallow Taiwan Strait. Taiwan was first isolated from the mainland by rising sea levels four to five million years ago (mya) and reached its present shape ca. 2 mya [6]. Previous biogeographic studies support that the many freshwater species easily migrates from the mainland to the island during Pliocene and Pleistocene glaciations as a result of the lowered sea level (e.g., [7, 8, 9, 10]). Geological evidence indicates that during glaciations, the land-bridges connected Taiwan Island to the Asian continent three to four times, initially in the Pliocene glaciation and potentially two to three times in the Pleistocene glaciation [11, 12]. Besides, during early and late Pleistocene, the sea basins of East Asian exposed and Korea, Japan Islands, Taiwan Island and mainland China connected [13, 14]. During ice ages, migrations between the Asian mainland and Taiwan, Ryuku Archipelago, and Japan may have been possible through land-bridges [15, 16]. The previous phylogeographical studies (e.g., [9, 17, 18]) suggest that the freshwater species in Taiwan might originated from mainland China and Japan in multiple times and by multiple colonization routes.

Previous phylogeographic studies [18, 19, 20] suggest that many geological barriers, e.g., the Central Range, Miaoli Plateau, and Kaoping foreland basins, shaped the structures and distribution patterns of the fauna in Taiwan Island. Taiwanese orogeny (mountain building) uplifted the longitudinal Central Range to nearly 4000 m (Figure 1). The distribution patterns and phylogeographic studies of freshwater fishes (e.g., [10, 19]) indicate that the Central Range may have acted as a barrier to dispersal between the western and eastern populations of the species. Lin [21] proposed that the Miaoli Plateau emerged at 0.150 mya based on geological studies, and many studies suggest that the Miaoli Plateau isolated the dispersions of freshwater fishes [9, 19]. The Kaoping foreland basins located in the southeast Taiwan Strait, reached a depth of 200 m within 3 km of shoreline [22]. Previous studies (e.g., [23, 24, 25]) proposed that this sea trench interrupted the extension of the Kaoping River toward the land bridge during glaciations. In other words, even during ice ages, the freshwater species in south of the Kaoping River could not cross the Kaoping foreland basins northward to the land bridge (Figure 1).

According to the geological history [11, 12, 13, 14] and phylogeographic studies [9, 17, 18, 26], our study found the freshwater species colonized Taiwan Island from Japan Islands or mainland China, through one or multiple routes, and one or multiple times. Moreover, the distribution patterns of the freshwater species contributed by the colonization origins, routes and times (e.g., [9, 19]). Thus, our study also wanted to know the distribution range of each *Neocaridina* species and their origins and phylogeographic patterns in Taiwan.

To address the above problems, the mitochondrial DNA (mtDNA) cytochrome c oxidase subunit I (COI) was used to investigate the genetic diversity and structure of the *Neocaridina* species in Taiwan. The sequences of mtDNA are usually analysed in studies of animal phylogeography (e.g., [9, 23, 27]). Among all the mtDNA genes, COI gene is a widely accepted marker to resolve the taxonomic identity and evaluate the levels of genetic diversity and differentiation in the Decapoda species (e.g., [28, 29]). The major questions in our study are (1) how many *Neocaridina* species are there in Taiwan, and (2) what is the colonization history of the *Neocaridina* species in Taiwan?

Results

Species diversity in Taiwan

Based on all COI sequence data in our study (Table 1) and Shih et al. (2017) [5], the ML tree (Figure 2) displayed that all sequences were assorted into 13 taxa (clades), and all sequences in Taiwan were assorted into four clades. The sequences of *N. davidi* in Taiwan, Kineme, Japan and Hawaii were grouped together, and close to *N. denticulata* in Japan. The sequences from mainland (populations CJ and HJ) were assorted into three species [*N. koreana*, *N. palmata*, and one undescribed species (*N.* sp. in China)]. The range of the pairwise genetic distance between these 13 clades of *Neocaridina* (Figure 2) was from 2.87% (between *N. davidi* and *N. denticulata*) to 15.23% (between *N.* sp. in Japan and *N. spinose*) (Table 2). The average of the pairwise genetic distance is 8.19%. These results suggested that there are four *Neocaridina* species in Taiwan, including *N. davidi*, *N. saccam*, *N. ketagalan* and one undescribed species

(*N.* sp. in Taiwan). *Neocaridina davidi* was distributed widely; *N. saccam* was distributed Central and South Taiwan; *N. ketagalan* was distributed North and South Taiwan; and *N.* sp. was only distributed East Taiwan (Figure 2).

Population and Demographic history

Although the phylogeny of *Neocaridina* species (Figure 2) displayed that there were four species in Taiwan, this study attempted to understand the colonization routes of these four species. Thus, this study proposed seven population history scenarios with the program DIYABC to understand the colonized history of the *Neocaridina* species in Taiwan. In the first scenario (scenario A), which was based on the phylogenetic analysis (Figure 2), these four species in Taiwan colonized by four different events (Figure 3a). Under scenarios B-D, according to the previous study (Ju et al., 2018) [26], the freshwater fish in East Taiwan was colonized from human. Thus, we proposed that the *N.* sp. might be originated from other three species (Figures 3b-3d). The scenario E (Figure 3e) showed that these four species colonized Taiwan by one colonization route and then divergent. In the scenario F (Figure 3f), *N. ketagalan*, *N. saccam* and *N. sp.* colonized Taiwan by the same colonization route and then divergent because these three species were allopatric. Finally, the scenario G (Figure 2g) displayed that two North Taiwan species, *N. davidi* and *N. ketagalan* colonized by one origin, and *N. saccam* and *N. sp.* colonized by one origin. The highest posterior probability was found for scenario A. Its posterior probability (D: 0.7560, 95% CI: 0.3795-1.0000; L: 0.9999, 95% CI: 0.9998-0.9999) was much higher than for other scenarios. The 95% CI of scenario A did not overlap with those for other scenarios (Figure 3). Thus, the *Neocaridina* species in Taiwan might colonize through four different events.

The time to coalescence was estimated in the BEAST analyses using two substitution rates, 2.33% per millions of years [2, 5, 30] and 1.1 % per millions of years [31]. The T_{MRCA} of these four species, *N. davidi*, *N. ketagalan*, *N. saccam* and *N.* sp., were 0.242-0.532, 0.37-0.774, 0.432-0.938 and 1.021-2.180, respectively (Table 3). Although, the estimated Tajima's D, and Fu's Fs were largely consistent within each species, excluding *N.* sp. (Table 3), none of the calculate values supported population expansion. Although the statistical analysis of the species-specific mismatch distributions (SSD and Rg indexes) revealed that the observed distributions were not statistically different from those expected under a sudden expansion model in all species (Table 3), the Bayesian skyline plots revealed that these four *Neocaridina* species in Taiwan declined recently (Figure 4).

Population diversity of Taiwan species

Neocaridina davidi

A total of 44 *N. davidi* COI haplotypes (641 bp) from 263 sequences were defined by 53 variable sites and 35 phylogenetically informative sites. The nucleotide sequences were A+T rich (60.0%). The mean COI haplotype diversity in each population was 0.47 (range: 0.00 to 1.00) (Table 1). The estimates of the current (θ_π) and historical (θ_ω) genetic diversity of each population indicated that most populations showed a pattern of decline ($\theta_\pi<\theta_\omega$) (Table 1). A comparison of the fixation indices N_{ST} and G_{ST} revealed that N_{ST} was larger than G_{ST} (0.72 and 0.47, respectively; Table 3). This result suggested a very weak relationship between phylogeny and geography.

Among 44 COI haplotypes, eleven haplotypes (D1-D11) were shared between two and more than two populations (Table 1). The most widespread haplotype was D9, distributed among nine populations. Among the 26 sampling populations, only one population (DA) had more than two shared haplotypes, and six populations (ML, DT, DJ, SA, DZ and GF) did not have any shared haplotypes. The population DA had the most shared haplotypes (D2, D3 and D9; Table 1). In the phylogenetic analyses, the haplotype trees reconstructed with different methods (ML and BI) were identical. In the BI tree (Figure 5a), 44 mtDNA haplotypes fell into three lineages (ND1-ND3). Lineage ND1 included 15 populations widespread in Taiwan, lineage ND2 contained five populations in North Taiwan, lineage ND3 contained nine populations in North, East and South Taiwan (Figure 5a).

In order to detect the ancestral region of *N. davidi* in Taiwan, all sampling populations were assorted as five regions as the previous studies, North (A), Central (B), South (C), Northeast (E), and East (D) Taiwan (e.g., [10, 32]). The results of the S-DIVA analysis produced a scenario with dispersion and vicariance events that shaped the current distributed patterns of *N. davidi* in Taiwan (Figure 5a). The ancestral populations of *N. davidi* were distributed in North, Central and Northeast Taiwan, and then divergent and dispersed widespread in Taiwan.

Neocaridina ketagalan

A total of 27 *N. ketagalan* haplotypes from 126 sequences were defined by 44 variable sites and 36 phylogenetically informative sites. The nucleotide sequences were A+T rich (58.2%). The mean COI haplotype diversity in each population was 0.49 (range: 0.00 to 0.75) (Table 1). The estimates of θ_π and θ_ω indicated that this species showed a pattern of decline ($\theta_\pi<\theta_\omega$) (Table 1). A comparison of the fixation indices N_{ST} and G_{ST} revealed that N_{ST} was larger than G_{ST} (0.82 and 0.44, respectively; Table 2). This result suggested a weak relationship between phylogeny and geography.

Among 27 haplotypes, four haplotypes (K1-K4) were shared between two and more than two populations (Table 1). Among these ten sampling populations, two populations (XH and DA) had two shared haplotypes, and four populations (ML, DT, LZ and JG) did not have any shared haplotypes. The haplotype trees reconstructed with different methods (ML and BI) were identical. In the BI tree (Figure 5b), 27 mtDNA haplotypes fell into three lineages (NK1-NK3). Lineage NK1 included three populations in North Taiwan;

lineage NK2 contained seven populations in North and Central Taiwan; lineage NK3 only contained on population (DS) in North Taiwan (Figure 5b). To detect the ancestral region, all sampling populations were assorted as three regions, A1, A2, and B (Figure 5b). The North Taiwan (A) were divided into two sub-regions (A1 and A2) by Taoyuan Plateau (Figure 1). The results of the S-DIVA analysis produced a scenario with dispersion events that shaped the current distributed patterns (Figure 5b). The ancestral populations of *N. ketagalan* were distributed north of Taoyuan Plateau, and then dispersed southward.

Neocaridina saccam and *Neocaridina species*

A total of eight *N. saccam* COI haplotypes from 47 sequences were defined by 17 variable sites and 15 phylogenetically informative sites. The nucleotide sequences were A+T rich (58.7%). The mean COI haplotype diversity in each population was 0.17 (range: 0.00 to 0.68) (Table 1). The haplotype and nucleotide diversities in the most populations were 0.00. This result displayed very high levels of differentiation among the populations. A comparison of the fixation indices N_{ST} (0.95) and G_{ST} (0.58) revealed a weak relationship between phylogeny and geography (Table 2). Among eight haplotypes, three haplotypes (S1-S3) were shared between two adjacent populations (Table 1). The haplotype trees reconstructed with different methods (ML and BI) were identical. In the BI tree (Figure 5c), all haplotypes fell into two lineages (NS1 and NS2). Lineage NS1 included four populations in south of Formosa Bank, and lineage NS2 contained two populations in north of Formosa Bank (Figures 1 and 5c). The results of the S-DIVA analysis displayed that the ancestral populations of *N. saccam* were distributed in north- (C1) and south (C2) of Formosa Bank (Figures 1 and 5c).

Six haplotypes from 43 sequences of *N.* sp. in East Taiwan were defined by 30 variable sites and 6 phylogenetically informative sites. The nucleotide sequences were A+T rich (59.1%). The mean haplotype diversity in each population was 0.30 (range: 0.00 to 0.53) (Table 1). A comparison of the fixation indices N_{ST} (0.28) and G_{ST} (0.51) displayed the most related haplotypes were found in different populations (Table 3). Compared within other species, N_{ST} of *N.* sp. is the smallest (Table 3). These results suggested that the level of population differentiation of *N.* sp. is lower than other three species greatly. The phylogenetic analyses also revealed population mixed (Figure 5d). The results of the S-DIVA analysis displayed that the ancestral population was distributed in population SK and then northward.

Discussion

Systematics of the genus *Neocaridina*

Many studies suggest that species should fulfil two criteria, monophyly and distinctness [33, 34, 35]. In the present study, the freshwater shrimp *Neocaridina* in Taiwan formed into four monophyletic clades (1, 6 9 and 12; Figure 2), and the mean genetic distance among these four clades was 6.64% (ranging 5.74% to 7.50%). The range of the pairwise genetic distance between these 13 clades of *Neocaridina* (Figure 2) was from 2.87% (between *N. davidi* and *N. denticulata*) to 15.23% (between *N.* sp. in Japan and *N.*

spinose), and the average pairwise distance was 8.19% (Table 2). Robe et al. [29] evaluated the utility of mtDNA COI in the species identification of Palaemonidae (Crustacea, Decapoda) and found that the mean genetic distances between species within the genus *Macrobrachium* ranged from 0.000 to 0.312 (mean = 0.198). Hebert et al. [36] suggested that the best threshold for distinguishing intra- from interspecific divergence was approximately 3% sequence divergence, although this value was later modified about ten times by many studies (e.g., [37, 38, 39, 40]). Thus, the present study suggested that the four clades in Taiwan corresponded to four species including *N. davidi, N. saccam*, *N. ketagalan* and one undescribed species (*N.* sp. in Taiwan) (Figure 2; Table 2).

Moreover, our study found that the systematics of *N. davidi* unidentified. *Neocaridina davidi* once named *N. denticulate sinensis* [5], and Shih et al. [2] suggested that it is synonymous to *N. davidi*. However, our study found that the genetic distance between *N. davidi* and *N. denticulata* was the smallest (2.87%). Thus, we could not suggest that "*N. davidi* in Taiwan" is a species or subspecies. Moreover, the systematics and distribution area of *N. denticulata* also unidentified. Accordingly, our study could not suggest the geological origin of *N. davidi* as other three endemic species, *N. saccam*, *N. ketagalan* and *N.* sp. in Taiwan. Our study suggested that the systematics and species diversity of the genus *Neocaridina* need revisions in future studies.

Multiple origins of the genus *Neocaridina* in Taiwan

Our study found four *Neocaridina* species in Taiwan. The distribution ranges of three species, *N. saccam*, *N. ketagalan* and *N.* sp., were restricted, and only *N. davidi* was widely distributed (Figure 2). The phylogenetic analysis of *Neocaridina* species in the world displayed that these four species in Taiwan are polytomous (Figure 2). The T_{MRCA} of these four Taiwan species were different (Table 3). Moreover, the results of the DIYABC demonstrated that these four *Neocaridina* species colonized Taiwan in four colonization events (Figure 3). Chang et al. (2016) [19] also found that two endemic *Microphysogobio* species colonized Taiwan from two origins and through two colonization centres. Previous studies (e.g., [9, 19, 41]) propose that, due to the geological history of Taiwan Island, the different colonization times shaped the different distribution patterns. These present results of the genus *Neocaridina* in Taiwan are agreement with those of previous studies (e.g., [9, 19, 41]).

Many studies (e.g., [9, 18, 19, 41]) suggested that when the freshwater species colonized Taiwan after the island reached its present shape, their distribution range were restricted. Among these four Taiwan species, *N.* sp. was restricted in East Taiwan. However, the distribution patterns of freshwater fishes and phylogeographic studies (e.g., [10, 19]) indicate that the Central Range have acted as a barrier to dispersal between the western and eastern populations of species. Thus, many freshwater species were not distributed in East Taiwan, and some species were distributed in East Taiwan by human activities [26]. Thus, the freshwater species in East Taiwan colonized before that in West Taiwan, or originated from populations in West Taiwan by human activities. The results of T_{MRCA} estimated displayed *N.* sp.

colonized before other species (Table 3). Based on the substitution rate of 1.1 % per millions of years [31], the T_{MRCA} of *N.* sp. was 2.180 mya, before the Central Range in Taiwan formed (ca. 2 mya). Moreover, the phylogenetic analysis of the genus *Neocaridina* displayed that *N.* sp. in Taiwan did not close to other species in Taiwan (Figure 2); and three *N.* sp. populations all have private haplotypes. Besides, the results of the DIYABC analysis also supported that the genus *Neocaridina* colonized Taiwan through four colonization events. Thus, this study suggested that *N.* sp. colonized Taiwan before island reached its shape, and the T_{MRCA} based on the substitution rate of 1.1 % per millions of years is likely a proper estimate.

According to previous studies (e.g., [9, 17, 18, 20, 26]), the freshwater species colonized Taiwan through five colonization centres, two in the south of Formosa Bank, two in the north of Formosa Bank and the south of Miaoli Plateau, and one in the north of Miaoli Plateau. In the phylogeny of the genus *Neocaridina* (Figure 2), *N. ketagalan* grouped with *N.* aff. *koreana* and *N.* sp. in Japan as monophyletic. The pairwise p-distance between clades of *Neocaridina* suggested that *N. ketagalan* was close to *N.* aff. *koreana* in Japan (Table 2). Moreover, the S-DIVA analyses showed that the ancestral populations of *N. ketagalan* were distributed in north of Taoyuan Plateau (Figure 5b). Thus, this study suggests *N. ketagalan* originated from Japan. *Neocaridina saccam* was only distributed south of Miaoli Plateau, and the results of the S-DIVA analysis demonstrated that the ancestral populations of *N. saccam* were distributed south- and north of Formosa Bank (Figures 1 and 5c). Based on these results, *N. saccam* did not colonize from Japan. According to the geographic locations, our study suggests that the *N. saccam* may have colonized from mainland China. Besides, although the S-DIVA analyses showed that the ancestral populations of *N. davidi* were distributed in northern Taiwan and the phylogenetic analysis displayed that *N. davidi* was close to *N. denticulata* in Japan, our study could not suggest the geographical origin because the systematics status of this species is unidentified (see DISCUSSION: Systematics of the genus *Neocaridina*). Accordingly, this study suggests that the *Neocaridina* species in Taiwan colonized through multiple geographical and temporal origins, but the deterministic geographical sources need more studies.

Population history of *N.* sp. in Taiwan

Our study found that *N.* sp. was only distributed in East Taiwan, and was distributed in three adjacent rivers only: SK, SM and WL (Figures 2 and 5d). Although the N_{ST} in this species was smaller than those in other species, only this species displayed the G_{ST} was higher than N_{ST} (Table 3). These results suggested that most related haplotypes were found in different populations. However, the depth of the sea around East Taiwan was deeper than the depth in West Taiwan (Taiwan Strait), and even during glaciations, these oceans around East Taiwan were not exposed. The previous studies displayed the amphidromous fish *R. giurinus* [42] and shrimp *Caridina pseudodenticulata* [41], larva survived in seawater, could not cross this deep sea. How did *N.* sp. colonize these three rivers? The geological study of Taiwan Island [43] proposed that these three adjacent rivers belonged to one river, the paleo-Siuguluan River (paleo-SK), and

separated after the middle Pleistocene. Thus, our study suggests that this species colonized Taiwan before this island reached its shape and then was isolated by the Central Range. Finally, it diverged by river diversion recently.

Phylogeography of *N. saccam* and *N. ketagalan*

Neocaridina ketagalan and *N. saccam* are allopatric distribution (Figure 2). *Neocaridina ketagalan* was only distributed west of Central Rang and north of the Wu River (excluding) (Figures 1 and 2), and the results of S-DIVA analysis showed the ancestral populations of *N. ketagalan* were distributed north of the Taoyuan Plateau (A1 region; Figure 5b). *Neocaridina saccam* was only distributed west of Central Rang, south of the Wu River (excluding), and north of Kaoping foreland basins (Figures 1 and 2). The S-DIVA analysis displayed that the ancestral populations of *N. saccam* were distributed in north of Formosa Bank (C1) and south of Formosa Bank (C3) (Figure 5c). Based on the distribution pattern and phylogeny of *Neocaridina*, (Figure 2), the results of the DIYABC analysis (Figure 3) and the results of previous studies (e.g., [17, 18]), *N. ketagalan* and *N. saccam* may have originated from Japan Islands and mainland China, respectively. The colonization routes of these two *Neocaridina* species, *N. ketagalan* and *N. saccam*, were similar to two clades of *Semisulcospira libertina* in Taiwan [18]. The populations in North Taiwan originated from Japan; the populations in South Taiwan may have originated from South China or South Asia.

Neocaridina saccam divided into two lineages, NS1 and NS2 (Figure 3c), exhibiting a southern and northern distribution, south- and north of Formosa Bank. The S-DIVA analysis displayed that the ancestral populations of *N. saccam* were distributed in south- and north of Formosa Bank (Figure 5c). Moreover, only two populations JS, the northernmost population, and ER, the southernmost population, have private haplotypes (Table 1; Figure 1). These results seem to reveal that the colonization route divided into two routes by Formosa Bank. The Formosa Bank is located at the south of Taiwan Strait. Previous studies (e.g., [9, 17, 19, 44]) have suggested that the Formosa Bank divided the glacial land bridge in the Taiwan Strait; however, the role of Formosa Bank on the population dispersion within the island has not been described. Ju et al. [26] proposed that during the maximum glacial periods, the ridge lifted from Formosa Bank to present coastal line of Taiwan Island. Therefore, during maximum glaciation, the dispersions between two sides of the bank through the exposed continental shelves of the island were broken. After *N. saccam* colonized island, the northward dispersal route was broken by the Miaoli Plateau, and the southward dispersal route was broken by the Kaoping foreland basins (Figure 1).

Neocaridina ketagalan can be divided into three lineages (NK1-NK3, Figure 5b). Lineage NK3 was restricted north of the Taoyuan Plateau; lineage NK1 was restricted in north of Miaoli Plateau; lineage NK2 was restricted north of Formosa Bank (Figures 1 and 5b). The S-DIVA analysis displayed that its ancestral populations were distributed in north of Taoyuan Plateau, and then southward (A1 region; Figure 5b). Finally, the population structure was shaped by Taoyuan Plateau, Miaoli Plateau and Formosa Bank. Taoyuan Plateau located in Northwest Taiwan (Figure 1). Some freshwater fishes, e.g., *O. evolans*,

Squalids argentatus, *Sinigrama macrops* and *Hemibarbus labeo*, were only distributed Tamsui River, north of Taoyuan Plateau (excluding). Chang et al. [19] and Hsu et al. [23] also found that Taoyuan Plateau divided the populations of *M. brevirostris* and *Semisulcospria libertina* as different lineages. Thus, the lineage NK3 was restricted in north of Taoyuan Plateau. Moreover, many studies suggest that the Miaoli Plateau isolated the dispersions of freshwater fishes [9, 19]. Thus, when Miaoli Plateau emerged, the populations were isolated and divergent (lineage NK1). Lastly, as the descriptions above, during maximum glaciation Formosa Bank and interrupted the migrations of *N. saccam* and *N. ketagalan*.

Population history of *N. davidi* in Taiwan

Among four *Neocaridina* species in Taiwan, the distribution range of *N. davidi* was wider than others (Figure 2). According to the previous study (e.g., [9, 18]), the widely distributed species colonized the Taiwan Island before the restriction species. However, the results of the T_{MRCA} analysis showed that *N. davidi* colonized island after other species (Table 3). Besides, our study also found this species distributed widely in the world. *Neocaridina davidi* is known to be an invasive species due to its importance in the aquarium trade (Englund and Cai for Hawaii [45]; Jabłońska et al. for Poland [46]; Klotz et al. for Germany [47]). Thus, some populations might result in the introduction to the wild by aquarium stocks.

Neocaridina davidi in Taiwan can be divided into three lineages (ND-ND3, Figure 5a). The lineage ND2 was only distributed in north of Miaoli Plateaus; lineage ND3 was almost distributed Northeast Taiwan; lineage ND1 was distributed widely. The results of the S-DIVA revealed that the ancestral populations were distributed in north of Formosa Bank and Northeast Taiwan. Moreover, our study found some populations did not have private haplotypes, and these populations were not distributed in ancestral areas, excluding population FG (Table 3; Figures 1 and 5a). Besides, the shared haplotypes of other three species were only distributed in neighbor populations, and the shared haplotypes of *N. davidi*, excluding D9 and D10, were also distributed neighbor populations (Table 1). Thus, we suggest the distribution widely haplotype and the discontinuous distribution might result in the introduction to the wild by aquarium stocks, and the transformations among wild population by human are rarer than the introduction to the wild by aquarium stocks.

In conclusion, our study considered the ancestral populations of *N. davidi* were distributed in north of Formosa Bank and Northeast Taiwan (Figure 5a), and then isolated and divergent by Central Rang and Miaoli Plateau. Finally, the lineages ND1-ND3 were restricted in Northeast Taiwan (E region), north of Miaoli Plateau (A region), and south of Miaoli Plateau and north of Formosa Bank (B region), respectively. We suggested the populations in regions C and D were might result in the introduction from aquarium stocks to the wild by human (Figure 5a).

Conclusion

This study found that there are four Neocaridina species in Taiwan, and they originated through four colonization events. There were five phylogeographic breaks in Taiwan, Central Rang, Taoyuan Plateau, Miaoli Plateau, Formosa Bank and Kaoping foreland basins. This study found that the population sizes of these four species all displayed population declining (Figure 4). In the census of Neocaridina species program in Taiwan, we found that the Neocaridina species is rare or disappeared in many rivers. Thus, the results of the present study provide information to conservation management agencies about the patterns of genetic diversity and the structure of Neocaridina species in Taiwan. However, this study does not solve the systematics of the genus Neocaridina in East Asia. The results of the present study provide information to the researches in the phylogeograpy in East Asia and the history of the genus Neocaridina. In the future studies, we need more sampling and more genetic characters.

Methods

A total of 479 specimens of *Neocaridina* species were collected from 35 localities in Taiwan, which almost covers all rivers within island (Figure 1; Table 1). *Neocaridina* species are not endangered or protected species and field works are conducted in accordance with guidelines established by the National Museum of Marine Biology and Aquarium in Taiwan. All specimens are lodged in the laboratory of Chiao-Chuan Han, National Museum of Marine Biology and Aquarium. The shrimps were collected from field sites with seines and fatally anesthetized with MS-222 (Sigma, St. Louis, MO). The samples were fixed and stored in 100% ethanol. Genomic DNA was extracted from the muscle tissue using the Genomic DNA Purification Kit (Gentra Systems, Valencia, CA, USA). The partial COI gene was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') [48]. Each 50 µl PCR reaction mixture contained 5 ng of template DNA, 5 µl of 10x reaction buffer, 4 µl of dNTP mix (10 mM), 5 pmol of each primer and 2U of Taq polymerase (TaKaRa, Taq polymerase). The PCR was programmed on an MJ Thermal Cycler as one cycle of denaturation at 94°C for 3 min, 40 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s and extension at 72°C for 1 min 30 s, followed by a 72°C extension for 10 min and 4°C for storage. The purified PCR products were sequenced using an ABI 377 automated sequencer (Applied Biosystems, Foster City, CA, USA). The chromatograms were checked with the CHROMAS software (Technelysium), and the sequences were manually edited using BIOEDIT 6.0.7 [49]. All new sequence data were submitted to GenBank (MG734216-MG734300). Moreover, in order to identify the *Neocaridina* species and find the originations of the genus *Neocaridina* in Taiwan, our study also download the sequences in Shih et al. [2] from GenBank (AB300177-90 and LC324764-79). Besides, our study also sampled some "*N. denticulata*" specimens in the Yangtze River (population CJ) and Hanjiang River (population HJ) in mainland China (Figure 1).

Sequence alignment and phylogenetic inferences

The nucleotide sequences were aligned in Clustal X 1.81[50]. The selection of the best-fit nucleotide substitution models was performed using the Bayesian information criterion (BIC) in jModelTest 2.0 [51]. The most appropriate nucleotide substitution model was HKY+I+G (Hasegawa-Kishino-Yano). Phylogenetic relationships among all haplotypes were inferred using Bayesian inference (BI) and maximum-likelihood (ML) in BEAST 1.8.0 [52] and MEGA 6 [53]. For the BEAST analysis, a stick clock model with a Bayesian Skyline tree was used. We ran 10^6 generations. Burn-in and plots for each analysis were visualized using Tracer v1.6 [54] to determine whether convergence and suitable effective sample sizes were achieved for all the parameters. The TREEANNOTATOR in the BEAST package was used to summarize tree data, and the tree was viewed using FigTree v1.3 [55]. For ML analysis, bootstrapping was performed with 1000 replications. In addition, the time to the most recent common ancestor (T_{MRCA}) was also calculated using the software package BEAST. The substitution rate of 2.33% per millions of years for terrestrial *Sesarma* [2, 5, 30] and 1.1 % per millions of years for Decapoda [31] were used.

Population genetic diversity

The intra-population genetic diversity levels were estimated using haplotype diversity (*h*) [56] and nucleotide diversity (θ_π and θ_ω) indices [57] in DnaSP v5 [58]. The current genetic diversity estimates (θ_π) were based on the pairwise differences between the sequences, and the historical diversity estimates (θ_ω) were based on the number of segregating sites among the sequences. Comparing the estimates generated by these two indices provides insight into the population dynamics over recent evolutionary history [58]. The existence of a phylogeographic structure was examined following the method of Pons and Petit [60] by calculating two genetic differentiation indices (G_{ST} and N_{ST}) in DnaSP.

Population history

To determine the potential diversification scenarios, a statistical dispersal-vicariance analysis (S-DIVA), which complements DIVA, was employed to determine the statistical support for ancestral range reconstructions [61]. The tree file formats were generated using the program BEAST. The range information was defined using the ichthyofaunal classification and phylogeographic studies (e.g., [10, 32]). The analysis was performed using the ‘maxareas = 2 to 5’ option (see RESULTS: Population diversity of Taiwan species; Figure 5).

Besides, the demographic histories were reconstructed using three different approaches. Firstly, we performed the Tajima's D and Fu's F_S neutrality tests [62, 63] in DnaSP. Under a population expansion model, significant negative values of Tajima's D and Fu's F_S were expected. Secondly, the mismatch distribution [64] was estimated under the assumption of a sudden expansion model as implemented in Arlequin version 3.5[65]. The sum of squared deviations (SSD) between observed and expected mismatch distributions and the raggedness index (Rg) were used as test statistics with 1,000 bootstrap replicates.

In the third approach, we reconstructed the historical demography using the coalescent-based Bayesian Skyline Plot approach (BSP) implemented in software package BEAST.

To reconstruct the unknown history of divergence, we performed approximated Bayesian computations (ABC) using DIYABC v.2.0 [66]. The DIYABC program enables the comparison of different historical scenarios involving population divergence, admixture and population size changes and subsequently infers demographic and historical parameters under the best-supported scenario. The reference table was built with 1,000,000 simulated data sets per scenario using the following summary statistics: one-sample statistics for number of haplotypes, Tajima's D, mean number of pairwise differences, variance of pairwise differences, and number of segregating sites; two-samples statistics for mean of within-sample pairwise differences, mean of between-sample pairwise differences, number of segregating sites and F_{ST} between samples. The uniform priors for all scenarios were used and no constraints to population sizes and coalescent times were given. All the scenarios were compared using direct (D) and logistic regression (L) approaches, and parameter estimation was performed only for scenarios with the highest posterior probability.

Abbreviations

COI: Cytochrome c oxidase subunit I; ML tree: Maximum- Likelihood tree; BI: Bayesian inference; SSD: the sum of square deviations; Rg index: the raggedness index; S-DIVA analysis: Statistical Dispersal-Vicariance Analysis;

Declarations

Acknowledgements

We thank Prof. Po-Hsun Kuo, Department of Industrial Management, National Taiwan University of Science and Technology, Taipei, Taiwan, for part of the data analysis.

Funding

This work was supported by grants from the National Museum of Marine Biology and Aquarium and the Taiwan's Forestry Bureau. The funding source had no role in the study design, collection, analysis and interpretation of data, writing the manuscript, or decision to submit results.

Availability of data and materials

All mtDNA sequences generated in this study have been deposited in GenBank under accession numbers: MG734216-MG734300.

Authors' contributions

CCH, LSF and IMC took part in fieldwork and performed molecular analyses. CCH, CCH, KCH and HDL interpreted the data, and drafted the manuscript. LSF and IMC designed the research, took part in some field works, polished the manuscript. All authors discussed the results, read and approved the final version of the manuscript for publishing.

Ethics approval and consent to participate

Ethical approval for this study was conducted in accordance with guidelines established by the National Museum of Marine Biology and Aquarium in Taiwan. No endangered or protected species were involved.

Consent for publication

Not applicable.

Declarations of interest to competing interest

The authors declare no competing interests in the preparation and execution of this manuscript. The authors are solely responsible for its content.

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Tables

Due to technical limitations, tables are only available as a download in the supplemental files section.

Figures

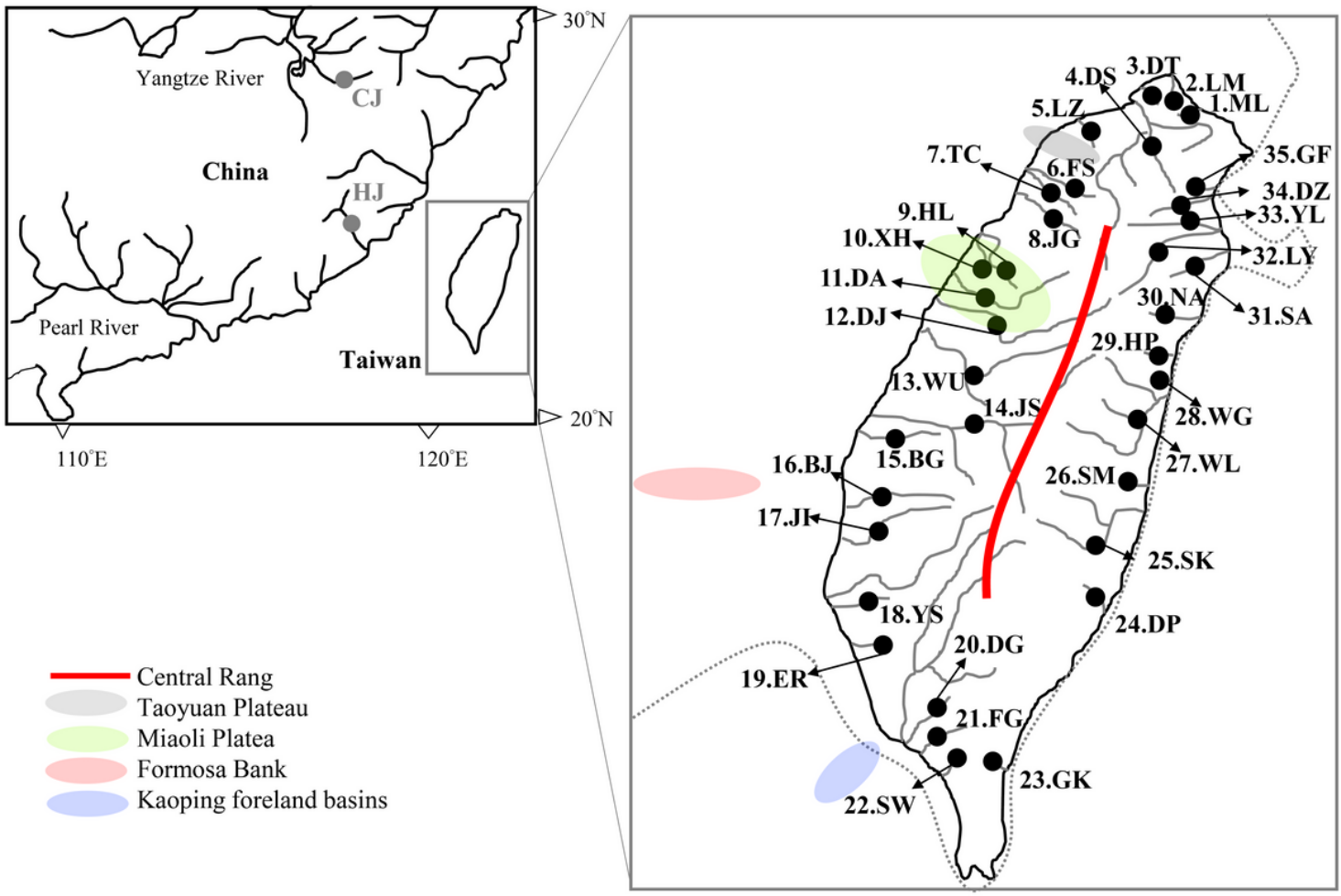

Figure 1

The sampling localities of the Neocaridina species in Taiwan are indicated by •

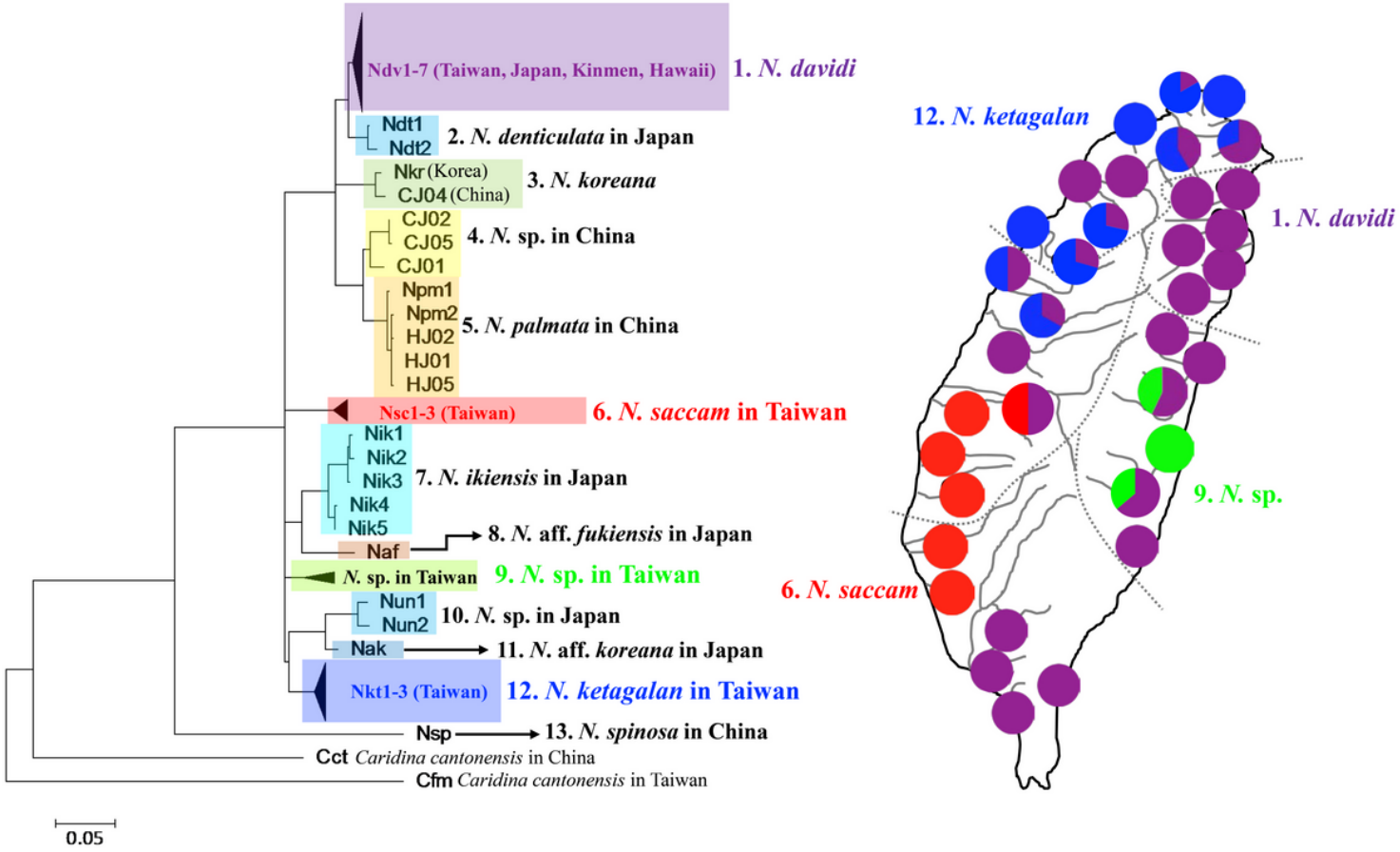

Figure 2

The ML tree of the mtDNA haplotypes in the Neocaridina species in Taiwan, China and Japan. The numbers at the nodes are bootstrap values

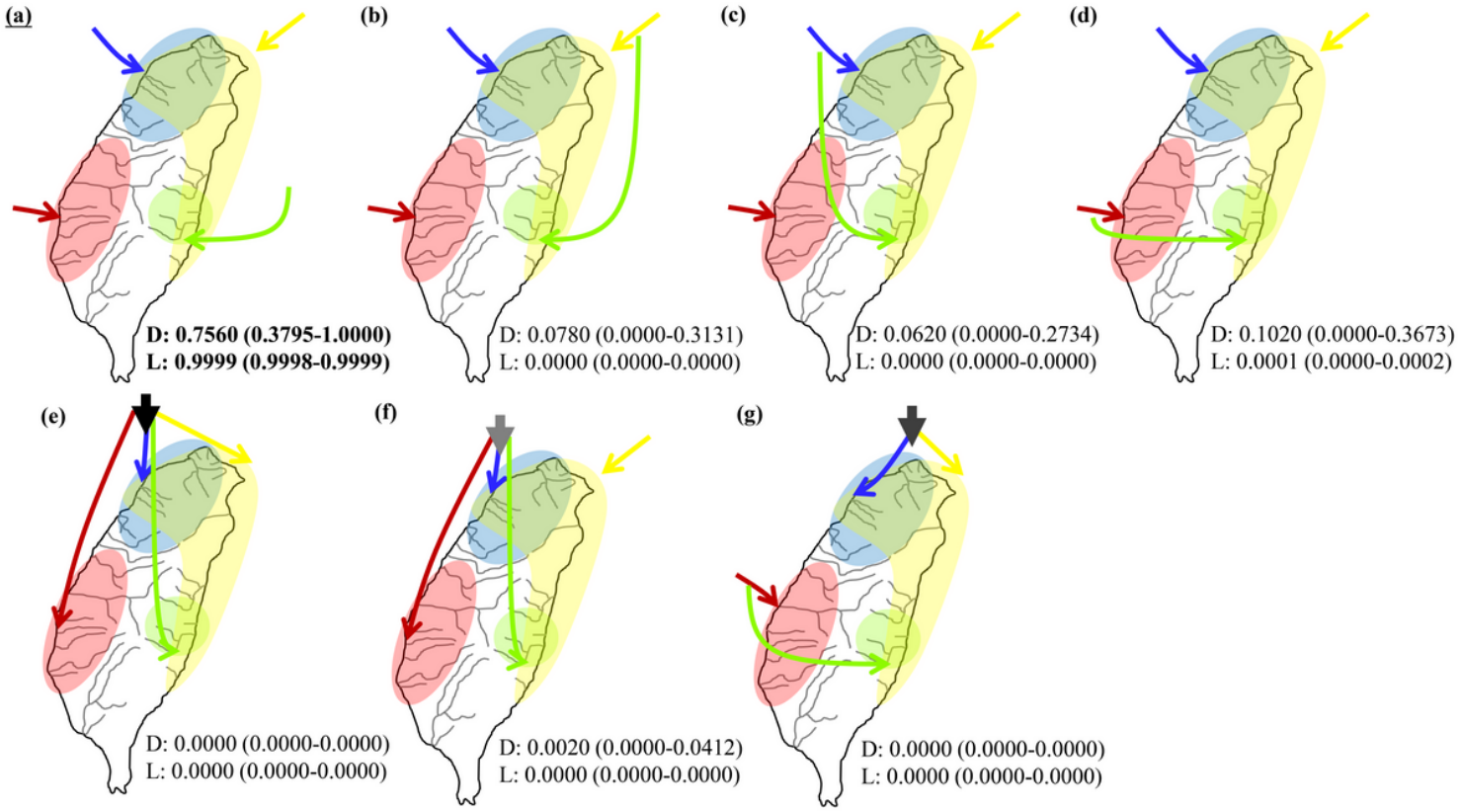

Figure 3

Graphical representation of the DIYABC analyses

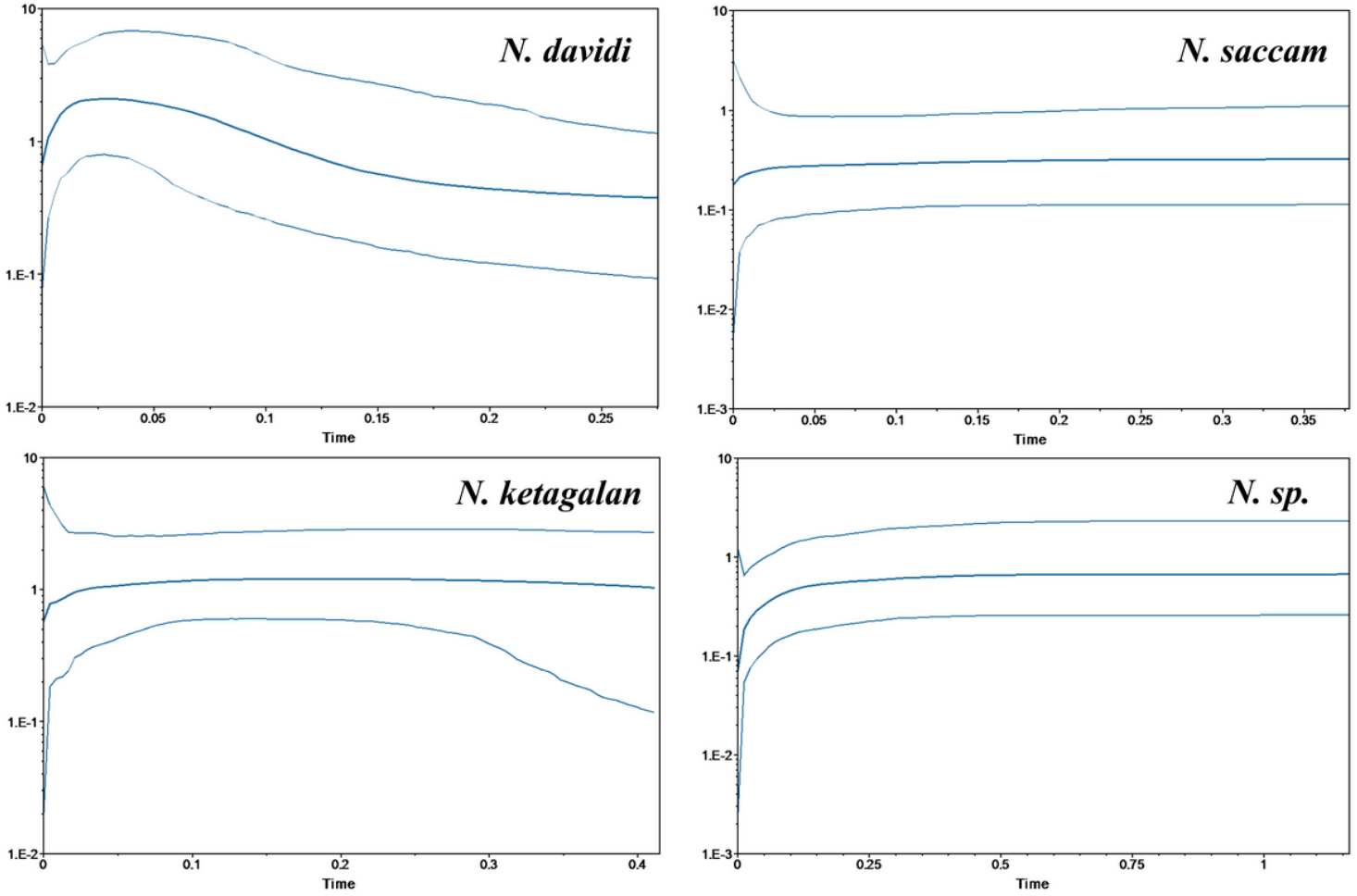

Figure 4

Bayesian skyline plot of the effective population sizes through time in N. davidi, N. ketagalan, N. saccam and N. sp in Taiwan

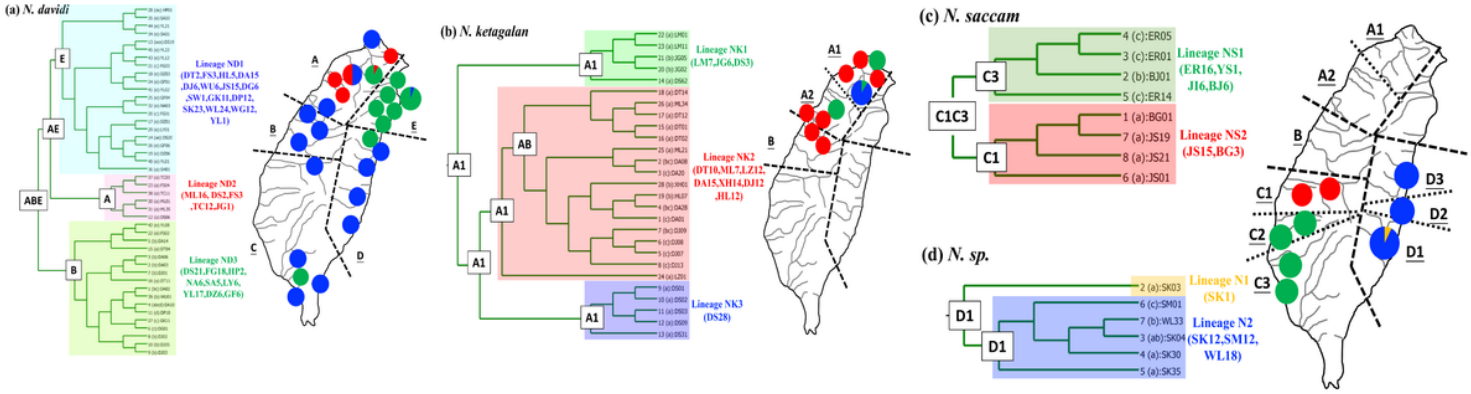

Figure 5

BEAST-derived chronograms of the mitochondrial DNA haplotypes of the (a) Neocaridina davidi, (b) N. ketagalan, (c) N. saccam and (d) Neocaridina sp. in Taiwan. The numbers at the nodes are bootstrap

values (maximum likelihood). The ancestral distribution inferred using S-DIVA is given in the box above each node. The frequencies of lineages in each population and the range information was displayed in map

Supplementary Files

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- supplement1.pdf